AN ABSTRACT OF THE THESIS OF

Teal M. Purrington for the degree of Master of Science in Rangeland Resources presented on January 29, 1992.

Title: Response of Wyoming Big Sagebrush (Artemisia Tridentata Ssp. Wyomingensis) to Defoliation of Understory Grasses and Drought.

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Water potential, leaf conductance, growth, nitrogen content, and seedling survival of Wyoming Big Sagebrush (Artemisia tridentata ssp. wyomingensis) following defoliation of the herbaceous understory were assessed during two growing seasons. Precipitation was 107% and 63% of the long-term mean (283 mm) in 1989 and 1990, respectively, which presented an opportunity to study impacts during a drought and a non-drought year. Response of Artemisia was measured on a site seeded to Agropyron desertorum in the late 1960s, and a native site with Stipa thurberiana, Festuca idahoensis and Poa sandbergii in the understory. The two sites were analyzed as separate experiments.

The dry year had a significant effect on plant water relations and growth of Artemisia on both sites. Pre-dawn

water potentials averaged 1.23 MPa more negative on the seeded site and 1.22 MPa more negative on the native site in 1990 compared to the previous year. Mid-day water potential averaged 1.22 MPa more negative on the seeded site and 1.13 MPa more negative on the native site in 1990 compared to 1989. Morning leaf conductance in 1990 was 61% lower on the seeded site and 51% lower on the native site than in 1989. Mean afternoon leaf conductance in the drought year was 62% less on the seeded site and 63% less on the native site. Nitrogen content in current year's growth was reduced 29% on the seeded site and 18% on the native site from 1989 to 1990. Vegetative and reproductive shoot (stem plus leaves) weights were reduced by over 80% in 1990 compared to 1989. Other production variables showed similar reductions in the drought year.

Nitrogen content was 11% greater in current year's growth from shrubs on control as opposed to defoliated plots on the native site in 1989. Shrubs on control plots had 8% heavier reproductive stems per unit of canopy, and 7% longer vegetative stems than shrubs on defoliated plots in 1989 on the seeded site. Shrubs on control plots had 18% fewer annual leaves per unit of vegetative shoot, but 12% more primary ephemeral leaves per vegetative shoot than shrubs on defoliated plots in 1990 on the seeded site. In 1990, shrubs on control plots on the seeded site had 11% more ephemeral leaves per vegetative shoot while shrubs on the

control plots on the native site had 8% fewer ephemeral leaves per vegetative shoot.

Large shrubs generally had more and heavier leaves, and longer and heavier stems than medium shrubs. Exceptions included large shrub lateral stems were 30% shorter than those of medium shrubs, and large shrubs had 37% fewer annual leaves per vegetative shoot than medium shrubs in 1989 on the seeded site.

Drought had substantial negative impact on water relations and growth of Wyoming big sagebrush, while defoliation of understory vegetation had little effect.

Response of Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) to defoliation of understory grasses and drought

by

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A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for
the degree of

Master of Science

Completed January 29, 1992

Commencement June 1993

Approved:

Redacted for Privacy

Professors of Rangeland Resources in charge of major

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Date Thesis is Presented: January 29, 1992

Typed By: Teal M. Purrington

ACKNOWLEDGEMENTS

First and foremost, I would like to thank my major professor Dr. Rick Miller, and co-major professor Dr. Paul Doescher, for their guidance, friendship, thoughtful suggestions, and for never doubting that I'd someday finish this project. It is to them I owe deepest thanks for my positive experience here as a graduate student.

I am also grateful to Dr. Tony Svejcar, Dr. Steve Radosevich, and graduate representative Dr. Elaine Ingham, for serving on my committee, providing helpful insight on thesis drafts, and for asking questions that made me think.

Jeff Rose, research assistant at the Eastern Oregon Agricultural Experiment Station in Burns, deserves special thanks for field work and statistical assistance far beyond the call of duty. I was truly lucky to have the help of someone as knowledgeable and generous as Jeff.

I would like to thank Paul Schmidt for his many hours of help with field work, and for teaching me to dig razor clams, jetty fish, and hunt.

My positive experience in the Range Department is also the result of numerous former and current fellow graduate students, who provided friendship, birthday cakes, late-night pool, swing-dance lessons and fishing trips that I'll always remember fondly. You know who you are -- Thanks.

I appreciate the entire crew at the Eastern Oregon Agricultural Experiment Station in Burns, for their

friendship, good humor, and patience with me and my sometimes impossible dog(s). Elaine LaChappelle and Arthel Ambrose deserve special thanks for cheerfully making sure my telephone calls and mail always reached me. The station provided lab and field assistance, equipment, a vehicle, and a place to live rent-free, for which I am grateful.

Cliff Michel provided invaluable friendship, guidance and direction, and set me off on an exciting journey. I will never be able to thank him enough.

My parents, Beverly Purrington and Foster Purrington, I thank for instilling in me at a young age an appreciation for scientific thought, and for always encouraging and trying to answer my "whys." Without this early training I'd never have made it here. To my brothers, Colin Purrington and Jesse White, thanks for being there, and for sharing your toys, and for being neat people I could admire.

And to my Mom and best friend, Beverly Purrington, and my step-father, Richard White, thanks for always being there, and for your encouragement and patience while I grew up. I could never have gotten here or through this without you.

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INTRODUCTION

Sagebrush (Artemisia tridentata Nutt.) is the most abundant and widely distributed shrub in North America. It is the dominant shrub characterizing the Intermountain Sagebrush Steppe, which covers 44.8 X 10^6 ha (Kuchler 1970). In the past 120 years Artemisia abundance has increased two to four fold at the expense of the herbaceous understory (Winward 1991).

Periodic anthropogenic disturbances including fire suppression (West 1978; Sneva et al. 1984, Miller 1988), overgrazing (Trlica 1977; Whisenant 1986), and other poor land management practices (Laycock 1967; West 1983; Miller et al. 1986) may also have enhanced Artemisia dominance throughout shrub-steppe communities. Uncontrolled livestock grazing of the herbaceous understory has been described as one of the primary factors attributing to the increase in Artemisia density and cover throughout the sagebrush steppe. Past research has primarily addressed the direct response of herbaceous plants to defoliation (see Caldwell et al. 1981, Richards 1984, Wraith et al. 1987, Ganskopp 1988). However, the indirect response of associated ungrazed plant species

within grazed plant communities has not been well documented.

Indirect responses to defoliation are those which occur in the soil and subsequently in the associated undefoliated plants as a result of the direct responses of the defoliated plants. Few studies have looked at indirect effects of grazing, such as decreased soil water depletion (Gifford and Springer 1980, Blackburn et al. 1982), reduced organic matter, increased erosion, and interspecific competition. Initial research indicates that indirect effects of grazing in the sagebrush steppe include increased Artemisia invasion (Pechanec et al. 1954, Hubbard 1957), growth (Weaver 1930, Pendery and Provenza 1987), and production (Laycock 1967). The indirect effects of defoliation are important because rarely do plant communities occur as monocultures, and rarely do all plants in a community receive the same grazing pressure.

Drought is another factor influencing competition in plant communities. Depending on the severity, timing and duration of drought, some species will be more affected than others. Little work has been done to quantify the response of Artemisia to drought, though climate in the Great Basin appears to have become more arid (Antevs 1948), and summer drought is a yearly occurrence. Periodic drought that reduces herbaceous plant cover (Pechanec et al. 1937, West et al. 1979) or vigor (Beetle 1960) may promote Artemisia

succession. Wallace and Romney (1972) alternately proposed that reduced competition for soil moisture during wet years might enhance Artemisia succession. It is possible that a combination of drought and wet years leads to Artemisia establishment.

A better understanding of relationships among plant species following drought and defoliation may help range managers predict changes in plant community composition, productivity, and stability (Branson et al. 1976, West et al. 1979, Menke and Trlica 1981, Caldwell 1985, Caldwell et al. 1985, Archer and Tieszen 1986, Svejcar and Christiansen 1987, Wraith et al. 1987, Miller et al. 1990). In our world of rapidly expanding population with associated increasing needs for resources, it is crucial that land managers understand how various disturbance factors influence rangeland plant communities. With this knowledge they can better manage unwanted vegetation, restore ecosystem function, and more productively and efficiently use and preserve natural resources.

The objectives in this study were to quantify specific responses in Artemisia tridentata ssp. wyomingensis caused by understory defoliation during a two-year period. However, due to the second year being particularly dry, the study was expanded to include assessing response of water relations, growth and nitrogen content of mature Artemisia tridentata ssp. wyomingensis and seedling survival under

drought conditions. The hypothesis was that soil moisture would increase on defoliated plots, resulting in improved water potential, leaf conductance, increased current year's growth, increased leaf nitrogen content, and higher seedling survival of Artemisia tridentata ssp. wyomingensis. We expected the drought year to produce essentially the opposite effects; water relations, growth, leaf nitrogen content, and seedling survival would all decrease.

LITERATURE REVIEW

Soil Moisture:

In the semi-arid sagebrush steppe in North America, water is generally the most important resource limiting plant growth (Weaver 1930, McKell and Goodin 1973, West 1983). Water is necessary for plant developmental and physiological processes, and it influences plant community structure (McKell and Goodin 1973).

Carbon dioxide enters a plant through openings in its leaves called stomata (Weatherley 1976). Open stomata allow not only influx of carbon dioxide, but also efflux of water. Water flows into roots by diffusion, through the plant by cohesive tension and active cell to cell transport, and out the stomata by evaporation. Water stress in plant tissues increases as the need for carbon dioxide, and thus open stomata and water loss, exceed water available in the soil. It is important for plants to avoid water stress, and maintain a relatively high water potential.

Growth reduction is the most sensitive plant response to lack of sufficient soil moisture (Levitt 1980), since cell expansion can not occur without turgor pressure. A plant under moisture stress produces growth retardants, and protein synthesis is reduced (Hsaio 1970). Under mild moisture stress, some plants reduce growth and shed foliage, thereby increasing root/shoot ratios (Pearson 1966, Davidson

1969). By retaining a favorable root/shoot biomass ratio plants may better survive drought. Reproductive growth is usually the most sensitive growth parameter. For example, following drought, A. viscida shrubs were shown not to develop flowers or produce seed, probably because energy (carbon) was allocated to vegetative survival (Parsons et al. 1981).

As water stress increases, photosynthesis and respiration are affected, although these responses are not as sensitive as growth (Levitt 1980). Early in the growing season, photosynthesis of semi-arid plants in the sagebrush steppe is limited primarily by leaf temperature and sunlight (Depuit and Caldwell 1973). With onset of summer drought, photosynthetic rate becomes increasingly limited by plant water status. A water stressed plant begins to close stomata, reducing photosynthesis. Intercellular space is reduced, slowing carbon dioxide movement through cells. As water stress becomes severe, photosynthetic pathways are damaged (Turner and Begg 1981). Though photosynthetic rate is reduced in a water stressed plant, selective stomatal closure increased water use efficiency (Tenhunen et al. 1990). Tenhunen et al. (1990) report that with increased temperature and decreased humidity, stomata in upper canopy leaves limit water use. This increase the contribution to carbon fixation from lower canopy leaves, which are shaded

by upper canopy and are therefore able to maintain higher water use efficiency.

Parsons et al. (1981) reported water potential did not differ between shrubs (A. viscida) lightly and heavily damaged by drought. They proposed shrubs compensated for low root turnover with root dieback or reduced new root growth, or both.

Sagebrush Seedling Dynamics:

The exact combination of environmental conditions favoring the establishment and survival of Artemisia seedlings is not known. However, the size, density and age structure of a population tell us something about the forces working on it (Pendery and Provenza 1987). Density is a function of seeds reaching an area (related to seed production and dispersal), seeds germinating, seedlings emerging, and seedlings and mature plants surviving. Kelsey (1986) states that "aside from germination data, very little information is available on the early growth stages of sagebrush seedlings, particularly in the field." Harniss and Murray (1973) indicate that more information is needed on Artemisia seed production and "the undefined weather variables that favor sagebrush seedling survival and establishment."

All stages of seedling life cycle have been shown to depend heavily on soil resources, especially moisture in

semi-arid lands. Wood et al. (1982) determined that moisture was the primary factor limiting Artemisia seedling emergence on semi-arid rangelands in the Great Basin. A study by Harniss and McDonough (1975) indicated that "good" years for Artemisia seedling establishment were not the result of merely good years for seed germination. Wallace and Romney (1972) theorized that wet years, or perhaps several in a row, were important for Artemisia establishment. Frischknecht (1963), too, believed wet years might reduce competition for water and allow Artemisia to establish, even in stands of crested wheatgrass (Agropyron cristatum). Beetle (1960) alternately proposed that drought might be responsible for promoting Artemisia invasion, by reducing vigor of grasses. West et al. (1979) reported highest densities of Artemisia following drought.

Shrubs have been shown to establish in areas where moisture or nutrients or both are concentrated, or during periods when resources are concentrated. Artemisia invasion may therefore be expected under shrubs, in a wet year after a drought, or when a disturbance has reduced competition for soil resources. Knowing what forces reduce vigor and increase mortality in Artemisia seedlings can be useful when planning control strategies aimed at this species.

Seed Production and Dispersal: The prolific seed producing ability of Artemisia has been shown to contribute greatly to its abundance (Harniss and Murray 1973). Goodwin

(1956) found that an Artemisia with a one meter canopy diameter, growing on shallow rocky soil produced an average of 335,000 seeds annually. On moister sites, such as deep loam soil, seed production was almost double that on drier sites.

Seed dispersal generally occurred from mid-October to mid-November. Dispersal was primarily by wind (Goodwin 1956), but beyond 30 m, other methods were usually responsible. The disseminule and pericarp are rough, enabling attachment to places like animal fur. This feature may have encouraged seeds to attach to rough soil surfaces, which would be beneficial since rough soil surfaces (litter, rocks, cracks, other plants) are likely to retain more moisture than other areas. Artemisia seeds floated due to an air pocket in the large pericarp, so dispersal by water was also possible.

Germination and Emergence: Artemisia has no dormancy mechanism (Goodwin 1956), no specific temperature requirements for germination (Harniss and McDonough 1975), and has the capability of germinating within 48 hours under sufficient soil moisture conditions. Researchers concluded that germination was most common in the spring (Pechanec 1954, Beetle 1955). Mueggler (1956) and Beetle (1955) reported that fall germination was rare except after disturbances.

Early germination is generally advantageous. It allows seedlings an early start on acquiring soil resources, establishing an extensive root system before soil moisture becomes limiting, and increases its competitive ability with other plants (Fowler 1988, Pendery and Provenza 1987). However, other studies have found an opposite effect; early emerging seedlings had lower survival (Klemow and Raynal 1981, Marks and Prince 1981, Mack and Pyke 1983). Premature emergence may have exposed a seedling to frost or predation it might not face later.

Since Artemisia seedlings were not very competitive with associated grasses (Goodwin 1956), disturbance probably played a major role in improving seed germination and seedling establishment. Studies by Johnson (1958) and Daubenmire (1970) showed that disturbances which removed or decreased the vigor of associated vegetation accelerated Artemisia invasion. High Artemisia invasion following brush control has been observed (Pechanec 1945, Mueggler 1956, Johnson 1958, Daubenmire 1970). Poulton (1950) concluded that sagebrush will come back on seeded range eventually if the range is grazed but not burned. After fire has temporarily removed vegetation, Artemisia seedling densities may initially be high (Mueggler 1956).

Seedling densities have been found to be highest in areas where evaporation was low or soil moisture was high or both. Wood et al. (1982) and Fuentes et al. (1984), found

more grass and shrub seedlings under shrubs than in interspaces between shrubs. They hypothesized that soil moisture may have been retained longer there due to shading. There are other reasons seedlings may be more common under shrubs; wind-dispersed seeds became trapped in litter under shrubs, and bird-dispersed seeds were deposited in shrubs used as perches (Fuentes et al. 1984). Although Fuentes et al. found more seedlings under shrubs than between shrubs, no seedlings survived in a dry year. In a very wet year, however, initial study indicated seedling survival under shrubs was approximately 50%, while seedlings between shrubs all desiccated within two months.

Sagebrush Adaptations to Limited Soil Moisture:

Vegetation in the Intermountain sagebrush steppe is adapted to repeated summer drought conditions, since little effective precipitation falls from July to August. The competitiveness of shrubs with other growth forms for soil moisture in this semi-arid region plays a major role in determining plant community composition (Miller 1988). Years of below average precipitation exacerbate the already arid conditions. Artemisia has a number of morphological and physiological adaptations which enables it to survive in a moisture-limited environment.

Plant water stress begins as transpiration exceeds water absorption. Water stress reduces plant water

potential, growth and survival (Weaver 1930). Plant growth response to drought may entail increased reproductive versus vegetative growth and germination inhibition; physiological adjustment may include seed priming, stomatal closure, and osmotic adjustment; morphological adaptations may include leaf area reduction, increased root/shoot biomass ratios, senescence, and spines or hairs to reduce water loss (Turner and Begg 1981).

In semi-arid rangelands, plant growth has been shown to be most limited by soil resources (McKell and Goodin 1973). Artemisia and perennial grasses competed heavily for these resources (Robertson 1943), as the majority of their root systems occupied the same soil profile (Campbell and Harris 1977, Sturges 1977). Artemisia obtained most of its moisture from the volume of soil within 910 mm of the plant, suppressing grass yield within that area (Frischknecht 1963). Robertson (1947) reported Artemisia's zone of moisture extraction extended to a radius of 1000 mm. Another study suggested that crested wheatgrass roots dominated Artemisia roots in the 200-500 mm depth (Caldwell and Richards 1986). However, Artemisia has a high root/shoot biomass ratio, and maintains roots at greater depth and lateral spread than most associated species, allowing it to extract water from a larger area than associated shallow-rooted species (Sturges 1977).

Miller and Shultz (1988) showed that one of Artemisia's most effective means of outcompeting other plants for soil moisture was its production of large ephemeral leaves early in the growing season. These leaves had lower leaf weight to surface area than annual leaves, and probably required less energy to produce. Ephemeral leaves also had higher leaf conductance rates than annual leaves (Squaw Butte Experiment Station file data). With high leaf area and conductance rate, sagebrush can capitalize on the relatively abundant spring moisture. As the season progresses and moisture becomes limiting, ephemeral leaves are dropped, and only the smaller more water-efficient annual leaves remain.

Similar periods of growth can also intensify competition between Artemisia and Agropyron desertorum (Frischknecht 1963). Although Artemisia is a C-3 plant and can photosynthesize at lower temperatures than most associated species (Caldwell 1978), it did not begin to extract moisture any earlier in the spring than Agropyron desertorum, also a cool-season plant. Miller (1988) showed that since Artemisia retained some leaves through the winter, it began the season with greater leaf area than associated species and could therefore deplete soil moisture faster in the spring (Miller 1988).

Artemisia was also able to remain physiologically active later in the season than many other species. Contributing to this is its ability to draw moisture from

dry soil with water potentials at -6 to -7 Mpa (Fernandez and Caldwell 1975). A shifting of root activity from surface to deeper soil horizons as it dries may also have allowed Artemisia to prolong its growing season. Another process which may have extended the period of adequate soil moisture for growth was "hydraulic lift," the nocturnal moving of water from deeper soil depths to surface soil by Artemisia roots (Richards and Caldwell 1987) .

Artemisia maintained a comparatively low photosynthetic rate (Mooney and West 1964, Dina and Klickoff 1973, DePuit and Caldwell 1973, Caldwell 1978), which can be a disadvantage in competitive interactions when water is not limiting. This disadvantage is offset by the maintenance of a higher leaf area than many of its neighbors during the growing season (Miller 1988). Also, in a semi-arid environment where drought is common, the ability to keep growing even in extremely low soil moisture conditions increases a plant's chance of successfully surviving dry periods (Depuit and Caldwell 1973, Dina and Klickoff 1973). Artemisia acclimated as the season progressed and was able to photosynthesize at higher rates as temperature gradually increased (Depuit and Caldwell 1973). Artemisia has sensitive stomatal control, but generally only used this method of controlling water loss after it had shed ephemeral leaves to reduce leaf area (Campbell and Harris 1977). Although Artemisia has a comparatively low water use

efficiency, this is not necessarily a disadvantage in areas it typically inhabits (Delucia and Heckathorn 1989). In competitive moisture-limited environments, heavy use of water when it is available may improve survival and enhance nutrient acquisition. This may be especially important in sagebrush systems, as water and nutrients are not evenly distributed in space and time (Schlesinger et al. 1990). The generally bare soil interspace between shrubs is susceptible to soil erosion, overland flow, high evaporation rate, and low nitrogen turnover. Artemisia accumulates nutrients and moisture under its canopy (Charley and West 1975 and 1977, Doescher et al. 1984), further exacerbating the patchiness of soil resources (Schlesinger et al. 1990). Nutrient caches can be particularly important in a drought, as a plant with nutrients readily available is at an advantage should precipitation occur.

Competition in Plant Communities:

Research has shown that increased competition for soil resources decreased growth (Ferguson and Basile 1967, Elliot and White 1987), reduced regeneration (Parker and Salzman 1985), increased seedling mortality (Hubbard 1957, Ueckert et al. 1979), and resulted in shorter, thinner, less branched roots (Ferguson and Basile 1967). Mueggler (1970, 1972) found that as competition increased, the detrimental

effects of clipping on Festuca idahoensis and Agropyron spicatum also decreased.

Competition can be visualized as "space" from which a plant can draw soil resources (Ross and Harper 1972). "Space" is essentially a measure of competition; a plant under intense competition is said to have less space than a plant facing lighter competition. Available space is a function of the "neighborhood" around a plant, that is, the number, size, health and spatial arrangement of neighboring plants. Few, small, unhealthy plants at a distance from a plant allow it more space than many large, healthy plants nearby. Different species will also present different levels of competition.

The density or number of neighboring plants affects the target plant's space. Increased density caused decreased production and number of flower stalks in Agropyron spicatum (Mueggler 1972). Welch and Jacobson (1988) found that changes in density of neighboring mature shrubs did not affect Artemisia seedling survival or seedling height.

Studies involving manipulation of density frequently involve removal of all surrounding vegetation. Romney et al. (1980) studied Artemisia seedlings on control sites and on sites where all vegetation had been killed by radioactive tests. They found seedlings were larger where competition from neighboring vegetation was negligible. On these sites, seedling size may have also been influenced by nitrogen

input from decaying dead plants. Increased tree growth following removal of surrounding grass was noted by Stuart-Hill and Tainton (1989). Conversely, they found increased grass growth after removal of trees. Removal of surrounding herbaceous vegetation caused elevated growth and stem number in Gutierrezia microcephala, a shrub of south-western North America (Parker and Salzman 1985).

Mature plants are also affected by changes in neighboring plant density. Manning and Barbour (1988) performed a study in which they removed vegetation around Haplopapus. Compared to plants on control plots, plants on treated plots had less negative (less stress) predawn water potentials. Predawn water potential in Chrysothamnus was unaffected by a similar treatment. Removal of surrounding vegetation resulted in higher leaf area, leaf water potential, and leaf conductance in Encelia farinosa shrubs (Ehleringer 1984). The author suggested shrub photosynthetic rates were also probably higher with neighbors removed. Stomatal conductance, root biomass and root length in a warm season Sonoran bunchgrass increased after removal of neighboring plants within 1.5 m (Robberecht et al. 1983).

Distance to and spatial arrangement of neighboring plants is another component of space. Bella (1971) found plant size affected by distance to neighbors, and Mack and Harper (1977) found distance to and spatial pattern of

neighbors responsible for 69% of weight and mortality variance in Bromus tectorum seedlings. Ehleringer (1984) reported increased growth with increased distance to neighbors. Other researchers found the opposite; seedling growth was higher when neighbors were closer. Matlack and Harper (1986) found young seedlings had higher survival, growth, and leaf number when neighboring plants were closer. A study by Fowler (1988) showed that having a juvenile plant within 20 mm was correlated with increased seedling survival and growth, compared to that of seedlings with no neighbors. Fowler believed that the neighbor did not have a positive influence on the seedling, rather that the neighbor indicated that it was in fact a good site for seedlings.

Age of neighboring vegetation can be a factor in competition. Blaisdell (1949) showed that as an Artemisia stand matures, it becomes increasingly difficult to establish grasses.

Available space is also a function of the species competing. Goodwin (1956) demonstrated that Artemisia seedling roots were not initially as efficient as those of associated species such as Agropyron desertorum and Agropyron spicatum. Several studies have shown Artemisia seedlings were unable to survive to the next season (Beetle 1955, West et al. 1979). Blaisdell (1949) found that good stands of Agropyron desertorum prevented establishment of

Artemisia seedlings, and that when present, Artemisia seedlings did not impair grass development.

Pendery and Provenza (1987) showed that Artemisia had increased current annual growth and number of inflourescences, and decreased mortality when grown in a monoculture as opposed to a mixture with other species. Robertson (1943) exposed populations of Agropyron desertorum and young Artemisia (four years old) to drought, and reported that grass was the only survivor in all replications. A shallow hardpan restricting deeper shrub roots may have given an advantage to the grass. Richardson et al. (1984) found that certain high rates of grass-broadleaf herb seeding (18-50 lbs grass:4 lbs herb per acre) prevented the establishment of Artemisia seedlings. Bleak and Miller (1955) concluded that seedlings of Artemisia and Agropyron desertorum did not have a significant effect on each other.

Several researchers have noted Artemisia seedlings were rare on native as opposed to seeded sites. Shantz and Piemeisel (1940) found only 6/100 m2 in Utah. Goodwin (1956) found less than 1/100 m2 in a native area, but 16-175/100 m2 in a wheat field across the road. Pechanec (1945) claimed 11/100 m2 was normal for most Artemisia grass vegetation. The scarcity of Artemisia seedlings on unseeded sites may have been due to low nutrient levels in soil and heavy competition from existing vegetation. Another

possibility is that predation on seedlings may be higher on unseeded sites.

Research has evaluated species-specific competition in other shrub species as well. Ferguson and Basile (1967) found complete mortality of Purshia tridentata seedlings on a site of native vegetation. However, their data on Purshia tridentata seedling growth indicated that seeded Agropyron desertorum and native vegetation provided essentially the same amount of competition.

Size of neighboring plants is another factor on available space. Larger neighboring plants were correlated with decreased target plant size (Bella 1971), decreased plant weight and increased mortality (Mack and Harper 1977). Stuart-Hill and Tainton (1989) found large trees more detrimental to grass growth than small trees. Weiner (1990) theorized larger plants obtained a disproportionately high share of resources compared to smaller plants, and that this would be reflected in community structure. He found decreased growth in plants with neighbors larger than them, while plants with neighbors smaller than them were not affected.

Direct Effects of Defoliation on Semi-Aridland Plants:

A considerable amount of work has evaluated the direct responses of plants to defoliation of aboveground foliage (McNaughton 1983, Caldwell 1984, Richards 1984. Research

has examined effects of herbage removal on above- and below-ground regrowth, on water relations, and on plant survival.

Roots of defoliated plants lose mass and decrease growth rates (Biswell and Weaver 1933, Crider 1955, Caldwell et al. 1981, Richards 1984, Svejcar and Christiansen 1987, Ganskopp 1988), leading to reduced absorptive surface. Weakened grass root systems may cause decreased drought tolerance (Hanson and Stoddard 1940, Weaver and Albertson 1943, Crider 1955), competitiveness (Svejcar and Christiansen 1987), winter survival (Weaver 1930), and cold and heat tolerance (Biswell and Weaver 1933, Julander 1945).

Above-ground production decreased as amount of defoliation increases. Mueggler (1972) reported production and number of reproductive stalks decreased as defoliation intensity increased, and Weaver (1930) noted tillering decreased under grazing pressure. Clipping grass during late vegetative stage in a dry year caused a 50% or more reduction in above-ground biomass production (Miller et al. 1989).

Plant water potential has been shown to increase with defoliation (Wraith et al. 1987). Photosynthetic rates in leaves regrowing after defoliation increased in a study by Caldwell et al. (1981), perhaps as plants reestablish a favorable root:shoot ratio.

Defoliation can ultimately result in death of the plant. Defoliation reduces plant vigor (West et al. 1979,

Stoddart 1946, Blaisdell and Pechanec 1949, Pearson 1964, Cook 1971), and can cause increased mortality (West et al. 1979). Mortality may be from reduced plant vigor caused by removal of leaves, but there are other possibilities. Herbivores can kill plants by uprooting, trampling, or burying them (Klemmedson 1977).

In some instances, defoliated plants may gain some advantage. Defoliation may rejuvenate senescent leaves (Hodgkinson 1974), increase tillering (McNaughton 1983), activate dormant buds (vanOverbeek 1977), improve water status of remaining leaves (McNaughton et al. 1983), or stimulate new growth (Trlica 1977). Microclimate and nutrient supply around defoliated plants may improve (Chew 1974, Owen and Wiegert 1976). Soil moisture may be retained later when plants are defoliated, thus prolonging the growing season or providing more moisture for regrowth or both (Svejcar and Christiansen 1987, Miller et al. 1989). The retention of soil moisture until later in the season may not occur in a competitive situation involving selective grazing, because ungrazed plants may quickly utilize unused soil resources.

Indirect Effects of Disturbances:

Disturbances including re-seeding, fertilization, fire, fire-suppression, grazing, and drought alter the distribution of soil resources, perhaps most importantly

soil moisture in semi-arid environments. Grazed plants use soil moisture less efficiently than ungrazed plants (Richards 1984), theoretically increasing water available to ungrazed plants in the community (Weaver 1930, Wraith et al. 1987, Miller et al. 1989). In this way, grazing indirectly influences the distribution of soil resources to different plant forms (Miller 1988), and shifts the competitive advantage to ungrazed plants (Mueggler 1970). Distribution of soil resources are further altered due to herbivore induced changes in energy flow and nutrient redistribution (Archer and Smiens 1991).

Plants adapt to herbivory either by avoiding it or tolerating it (Archer and Smiens 1992). While grasses are generally grazing tolerators, and are able to survive herbivory, they are often at a competitive disadvantage when in competition with grazing avoiders. Artemisia is not a grazing tolerant plant, but it is well adapted to avoid herbivory. Unpalatable secondary compounds in its tissues discourage herbivory. By avoiding herbivory, Artemisia can gain a competitive advantage for limited moisture in grazed plant communities (Caldwell 1978). Under continued improper grazing management, shrubs can increase their size and abundance in the community at the expense of other more desirable plants (Pickford 1932, Whisenant 1986).

Grazing can have an indirect effect on plant invasion. In undefoliated areas, moisture may be tied up by existing

vegetation such that woody species are unable to invade (Stuart-Hill and Tainton 1989). After a disturbance such as herbivory, soil moisture and nutrients are more available to remaining or invading plants (Robberecht et al. 1983). In wet years competition for soil water may be minimal.

Sagebrush seedlings have been reported to invade ungrazed crested wheatgrass stands during wet years (Frischknecht 1963). In an area previously sprayed, Hubbard (1957) found no Artemisia seedlings in an area exclosed to cattle but 14 to 53 seedlings per plot in grazed areas (plot size 1/10 to 5 acres). Heavy grazing "accelerates sagebrush reinvasion" Pechanec (1954). Grazing has been shown to allow some sagebrush invasion into newly seeded areas (Richardson et al. 1986), perhaps by reducing competition for soil resources or light. However, Brown and Archer (1987) monitored mesquite seedlings and found higher densities on areas with no cattle. Grazing does not always enhance shrub invasion; Reed and Peterson (1961) showed grazing in an Artemisia community had little effect on species composition. Laycock (1967) found sheep grazing did not affect density of Artemisia seedlings or shrubs under 150 mm.

Grazing removed biomass and therefore decreased litter (Tomanek 1948, Reed and Peterson 1961). Plant litter on the ground reduced evaporation and runoff, increased infiltration and nutrient cycling, and was important for

seed germination (Tomanek 1969). Evans and Young (1970) found litter had a positive effect on seedling survival in arid environments. However, litter had a negative effect on survival of native grass seedlings in a Texas grassland (Fowler 1988). Beetle (1955) believed litter inhibited Artemisia seedling germination and establishment.

A number of studies have shown that defoliation of surrounding plants improves health of associated undefoliated plants. Artemisia growth, number of flower stalks, and survival increased when understory Agropyron desertorum was defoliated (Pendery and Provenza 1987). Laycock (1967) reported increased production in Artemisia tripartita (60-78%) and decreased grass production under heavy spring sheep grazing. Artemisia growth often more than doubled after defoliation of neighboring vegetation (Weaver 1930).

Underground plant parts are also affected by selective defoliation. Root growth and distribution may increase when competition is reduced through defoliation of neighboring vegetation (Robberecht et al. 1983).

Defoliation of neighboring plants does not always have a positive effect on associated undefoliated plants. A study in South African semi-arid savanna by Stuart-Hill and Tainton (1989) revealed that defoliation of trees reduced grass production as much as 40%. In the reverse situation, grass defoliation had no effect on tree growth. The

researchers presented two hypotheses for the negative response to neighbor defoliation: 1) undefoliated trees provided more protective shade than defoliated trees (Walker 1974), and 2) undefoliated trees "pumped" water from deep soil to surface soil where grasses could utilize it (Bosch and Van Wyk 1970).

Few studies have evaluated water relations in plants when understory vegetation has been defoliated. Branson et al. (1976) found no large differences in plant water potential between grazed and ungrazed areas.

Competitive interactions occurring between species are changed when grazing is introduced to the system (Archer and Tieszen 1986). Herbivores changes species composition (Svejcar and Christiansen 1987), but the "complexity of interactions among various abiotic and biotic factors within the ecosystems and the feedback control which governs them" makes it difficult to predict the direction of change (Trlica 1977). Grazing pressure will also favor plants which avoid grazing over plants which are merely able to tolerate it (Archer and Smiens 1991). Community dominance is shifted from palatable grasses and forbs to unpalatable species, including Artemisia (Pickford 1932). Ungrazed plants live longer than grazed plants (West et al. 1979), thereby retaining dominance of an area.

STUDY SITE DESCRIPTION

Location and History:

The study was conducted at the Squaw Butte Experimental Range Station in southeastern Oregon, which is located 67 km southwest of Burns, in the northwest corner of Harney County (119° 43′ West latitude, 43° 29′ North longitude). The station lies in the far northern portion of the Great Basin, and is representative of shrub-steppe rangeland ecosystems dominated by Artemisia. This ecosystem type occurs in a large portion of southeastern Oregon, as well as in many areas of adjoining states (Kuchler 1970). The Squaw Butte Range is jointly owned and operated by the U.S.D.A. Agricultural Research Service, and Oregon State University. It was established during the drought of the 1930's, and encompasses a total of 6,580 hectares, with elevation ranging from 1,373 to 1,678 m. The land was used as wild horse range until the 1920's, and as sheep lambing ground from then until 1935. Poorly managed grazing, especially in early spring, resulted in degraded rangeland (Sneva et al. 1984).

Climate:

The climate is cool, semi-arid desert, characterized by large seasonal variations in temperature and moisture (West 1983). Winters are cold and wet, summers hot and dry. The

mean winter temperature is -0.6°C, with a daily minimum of -4.8°C. During summer, temperatures average 17.6°C, with daily maximum of 26.8°C. Although the average frost free period is 80 days each year, frosts can occur in mid-summer. The area receives 283 mm of precipitation annually (39 year mean), of which 80% occurs October through June, mostly as snow. Soil moisture recharge during the summer is rare. Consequently, the highest plant growth rates occur in the spring with many species becoming quiescent by early to mid-summer.

Geology and Soils:

Soils at the study site are coarse to fine sandy loam, frigid Orthidic Durixerolls of the Milcan Series (Lentz and Simonson 1986). The site is an ancient flood plain and stream channel on a 0-2% slope near the base of Squaw Butte, an early Pleistocene volcano. The soil is well drained and is underlain by a duripan at 0.5 to 1.0 m.

Vegetation:

Native vegetation of the area is representative of the sagebrush-steppe. The dominant shrub is Artemisia tridentata ssp. wyomingensis, with some Chrysothamnus viscidiflorus ssp. viscidiflorus. Grass species include Festuca idahoensis, Agropyron spicatum, Stipa thurberiana,

Poa sandbergii, Sitanion hysterix, Agropyron smithii, and Bromus tectorum. (Lentz and Simonson 1986).

The two study sites contain differing vegetation. Both sites are dominated by Artemisia tridentata ssp. wyomingensis, but one has native understory vegetation, while the understory on the second site is dominated by Agropyron desertorum, seeded in the 1960s. We refer to these sites as the "native" and "seeded" sites.

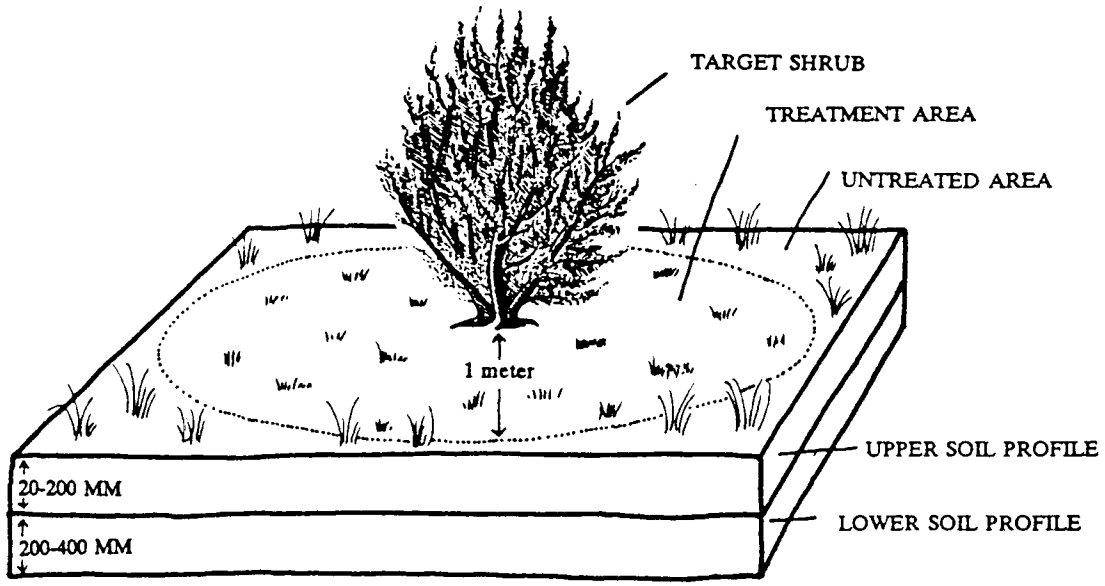
EXPERIMENTAL PROCEDURES

Mature Shrub Plots:

Experimental Design: A split-strip plot design was used on both the native and seeded sites. Strips were treatments, split by shrub size classes. The native and seeded sites were analyzed as separate experiments. Plot selection within sites was random. Criteria used for plot selection were that Artemisia plants had full vigorous canopies and that deep-rooted perennial grasses were present within 1 m of the shrub center. This selection reduced variation by maximizing homogeneity between plots. Plots extended to 1 m in all directions out from the center shrub (see Figure 1). Artemisia were selected from three height classes; "small" shrubs were <150 mm, "medium" shrubs were 150-300 mm, and "large" shrubs were >300 mm.

Twenty each of medium and large shrub plots from each site were selected in 1989. In the second year, 20 new medium and large shrub plots were selected on each site to avoid introducing error from a second year of destructive sampling. On each sampling date, half the plots were measured within each site X size X treatment combination. Forty small shrub plots were established on the seeded site the first year, and sampling alternated between four sets of 10 of these plots each sampling date,

a) Mature Shrub Plot Layout



b) Shrub Seedling Plot Layout

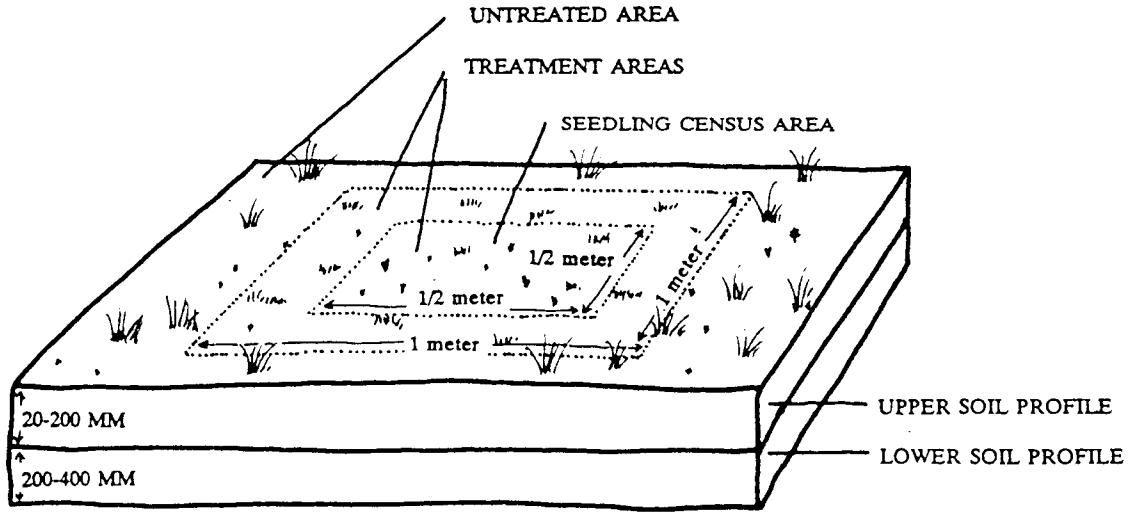


Figure 1. Plot Layout for a) mature shrubs and b) seedlings.

each year. No small shrubs were marked on the native site, since few shrubs under 150 mm were present.

Treatments: Defoliation treatment was applied at two levels; control plots received no defoliation, while defoliated plots had understory vegetation clipped to a 25 mm stubble height. Half the plots on each site and within each size class were randomly selected for defoliation. Clipping was performed in early-May during the early boot stage, using a weed-eater. Grasses and forbs growing under Artemisia canopies were not defoliated, with the assumption that these plants would not be grazed under actual livestock grazing.

Measurements:

Weather: Precipitation and air temperature were obtained using a U.S. Weather Bureau Station located about 1 km from the study site. On-site photosynthetically active radiation, temperature and relative humidity were measured with a Licor LI-1600 steady state porometer. Measurements were collected in both years, every two weeks from June 1 to the end of July, and once at the end of August, concurrent with plant and soil measurements.

Soil Moisture: Soil water content was determined gravimetrically at two depths from five plots within each treatment X size combination on each site. Samples were taken at the 20-200 and 200-400 mm soil horizons. On the next date, the remaining five plots from each treatment X

size combination were sampled. Sampling alternated between the two sets each date. For small shrub plots, sampling alternated between four sets of 10 plots, each set containing five control and five defoliated plots. Later in the season, as soil dried and hardened, it was not always possible to obtain soil samples from the deeper horizon.

Soil samples were collected within plots in the shrub and grass interspaces. To minimize disturbance and assure correct readings, previously sampled spots were avoided. Each sample was placed in a tightly sealed can, and weighed to the nearest tenth of a gram. Samples were dried at 170°C for at least 48 h, then weighed to determine percent moisture. Sampling was performed every two weeks from early June until the end of July, and once in late August.

Soil moisture release curves were developed for an adjacent site and used to convert percent soil water to soil water potential.

Plant Water Status: Plant water measurements were recorded on five medium and five large shrubs for each treatment on each site concurrently and in the same plots as soil moisture samples. Plant water measurements would have been relatively too destructive for small shrubs, and were therefore only collected from medium and large shrubs. Pre-dawn and mid-day plant water potential measurements were measured between 0400 and 0500 and 1200 to 1500 h, respectively. Five Artemisia terminal vegetative shoots

were collected from each treatment for each size class on each date. The sample was immediately sealed in a ziploc plastic baggie, placed in a cooler with ice, and measured with a pressure bomb (Scholander et al. 1965) within 45 minutes of collection.

Leaf conductance was measured between 0730 and 0900 h, and 1200 and 1500 h. Conductance, temperature, relative humidity, and photosynthetically active radiation were measured with a Licor LI-1600 steady state porometer. Conductance was measured on the same branchlet in the morning and afternoon. After measurements were complete, the branchlet was removed, stored in a plastic baggie in a cooler on ice, and transferred to a freezer. Leaf area was determined later with a Licor LI-3100 leaf area meter. The stem was not included in this measurement.

Growth: Current year's production for medium and large shrubs was determined for a variety of growth parameters. I collected up to five each of current year terminal vegetative shoots (stems plus leaves) and reproductive shoots (stems plus leaves plus flowers) from each plot in early-July. At this date, shoot elongation and leaf production should have ceased (Miller and Shultz 1987). Length and dry weight of terminal and lateral stems, and dry weight of leaves were determined. Leaves were separated as annual, primary ephemeral, or secondary ephemeral on vegetative stalks. In late August, reproductive shoot

density was determined for all three shrub size classes. A 200 x 200 mm frame was placed in the top center of each medium and large shrub, and the number of reproductive shoots in the frame were counted. For small shrubs, all reproductive and vegetative shoots in the entire canopy were counted. Canopy area was estimated by measuring the longest and shortest diameters (canopy area = pi X diameter1 X diameter2 / 4).

Nitrogen Content in Current Year's Growth:

Current year's leaves and stems from medium and large shrubs were collected in early July from each plot. Samples from medium shrubs were "paired," so that less material had to be removed from each of these shrubs. Pairing was between two nearby shrubs on the same site, with the same defoliation treatment. Samples were dried for 48 h at 60°C, then ground and analyzed by semimicro-Kjeldahl method (Bremmer 1965) for nitrogen content.

Statistical Analysis: Data were analyzed as a strip-split plot for each of the two sites within years. Defoliation treatments were the strips, split by size classes. Significant differences for variables between dates, treatments, sizes and years were identified by analysis of variance using SAS (1987). When F values indicated significance ($P \leq 0.10$) using ANOVA, least significant differences (LSD) were calculated (Steel and Torrie 1980). Interaction between treatment, time, and size

were tested. Due to non-homogenous variability across data, ANOVA was not always appropriate. T-tests were therefore used for some water relations data. In all cases, only significant differences are reported in the text.

Shrub Seedling Plots:

Experimental Design: The experiment was laid out as a completely randomized design with a total of 20 m^2 plots. Measurements were recorded in the center quarter meter of the plot, and the outer 3/4 meter was used as a buffer (see Figure 1). Criteria used for selecting seedling plots was presence of at least 10 seedlings in the center quarter meter of the plot, and absence of mature shrubs in the whole plot. Seedling plots were located only on the seeded site, since Artemisia seedlings were rare on the native site.

Treatments: Half of the seedling plots were randomly selected for the defoliation treatment, while the remaining half served as the control. Defoliation was at the same time, and to the same extent as for mature shrub plots. Plots were clipped with hand clippers, rather than with a weed eater, to prevent damage to Artemisia seedlings.

Measurements:

Soil Moisture: Five plots within each treatment were sampled for soil water content. Samples for soil moisture samples were collected similarly and concurrently

with soil moisture samples collected in the mature shrub plots. Samples were collected in the buffer portion of each plot.

Density: *Artemisia* seedling density was recorded in the center quarter meter of each plot every two weeks from mid-May to the beginning of September.

Statistical Analysis: Significant differences for variables between dates and treatments were identified by analysis of variance, acsine transformation, and repeated-measures analysis. Significance was determined at $P \leq 0.10$ using ANOVA (Steel and Torrie 1980). Interaction between treatment and time were tested for.

RESULTS

I. Defoliation Study -- Mature Shrub Plots:

Environmental:

Weather: Precipitation was 302 mm from September 1988 to September 1989, 106% of the 39 year mean (283 mm) (Figure 2). In the 1989-1990 year, precipitation was only 189 mm, 67% of the long term mean (Figure 3).

Soil Moisture: Soil moisture content in the 20-200 mm soil profile declined gradually through the 1989 and 1990 growing seasons (Appendix Tables 1 and 2). Field capacity (-0.03 MPa) in the 20-200 mm soil profile was 23% soil moisture content, and wilting point (-1.5 MPa) was 9% soil moisture content. In early June of 1989, soil moisture in the upper soil profile was about 11%, dropping well below -1.5 MPa by late July. In 1990, a drier year than 1989, soil moisture was near -1.5 MPa in early June and declined to well below -1.5 MP in late July. In late August of both years, soil moisture increased slightly due to late August precipitation. No significant differences in soil moisture content were detected between control and defoliated plots, or between medium and large shrubs. Soil moisture data for the lower soil profile, 200-400 mm, is shown in Appendix Tables 3 and 4.

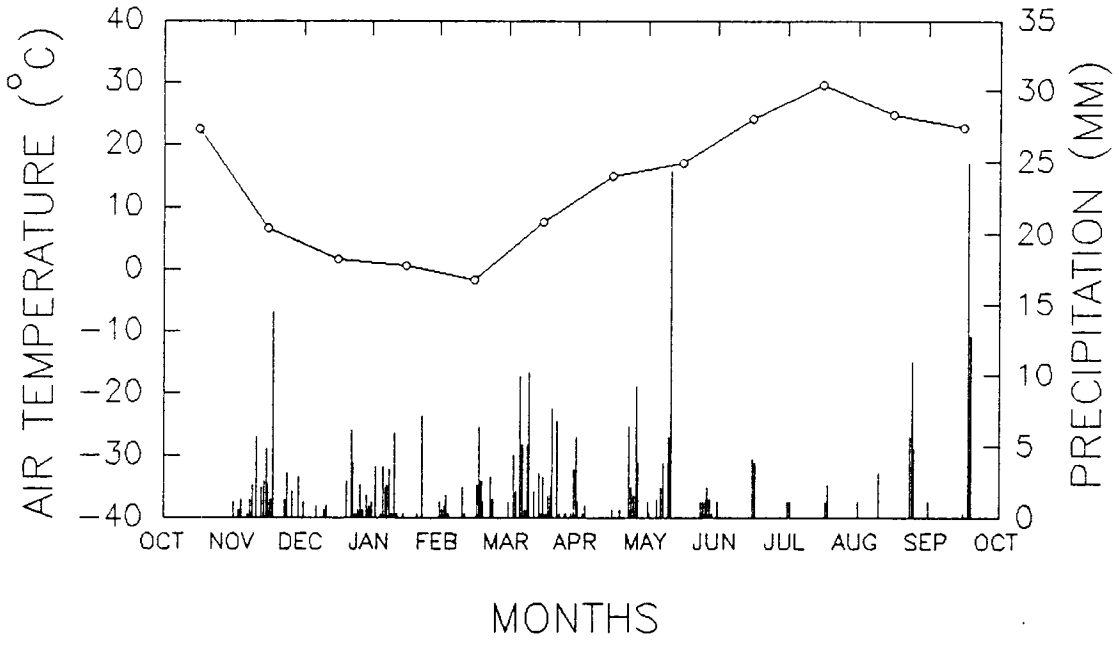


Figure 2. Air temperature (°C) and precipitation (mm) during the 1988-1989 year.

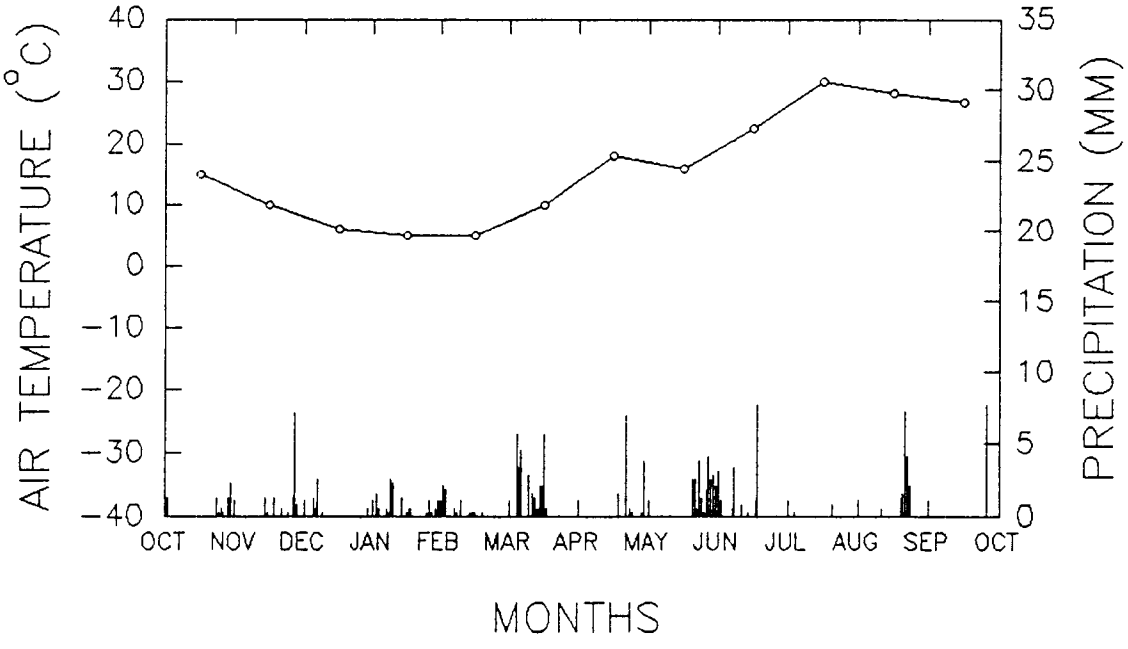


Figure 3. Air temperature (°C) and precipitation (mm) during the 1989-1990 year.

Plant Water Relations:

Plant Water Potential: Both pre-dawn and mid-day plant water potentials decreased (plants became more stressed) from June through the end of July and increased in late August due to increased soil moisture and cooling temperatures (Appendix Tables 5 and 6). This trend occurred in both years on both sites. Pre-dawn and mid-day water potentials of large shrubs were equal or significantly lower than medium shrubs on all but one date (Tables 1, 2, 3 and 4). No differences were detected between plants on control and defoliated plots.

Leaf Conductance: Morning and afternoon conductance values in 1989 decreased as the growing season progressed, then increased in late August (Tables 5, 6, 7 and 8). In 1990 the pattern was slightly different; conductance decreased substantially from the first to second sampling dates, then increased each date through late August (Appendix Tables 7 and 8). Morning and afternoon conductance was more frequently significantly greater for medium shrubs than large shrubs on both the native and seeded sites. No differences were detected between control and defoliated plots.

Table 1. Plant water potential (MPa) at pre-dawn (0400-0500 h) and mid-day (1200-1500 h) for large and medium shrubs on the seeded site through the 1989 growing season.

PRE-DAWN:

Date	Medium	Large	Difference	LSD	
June 1	- .70	- .68	+ .02	.07	NS
June 12	- .88	- .80	+ .08	.09	NS
June 28	- .92	- .90	+ .02	.15	NS
July 14	-1.08	-1.31	- .23	.09	*
July 29	-1.49	-1.67	- .18	.32	NS
August 31	-1.15	-1.38	- .23	.14	*

MID-DAY:

Date	Medium	Large	Difference	LSD	
June 1	-1.52	-1.46	+ .06	.20	NS
June 12	-1.74	-1.86	- .12	.09	*
June 28	-1.74	-1.76	- .02	.10	NS
July 14	-1.95	-2.31	- .36	.15	*
July 29	-2.49	-2.74	- .25	.33	NS
August 31	-2.04	-2.69	- .65	.27	*

*: Significant difference at $P \leq .10$ between shrub size at that date; NS: Not significantly different at that date.

Table 2. Plant water potential (MPa) at pre-dawn (0400-0500 h) and mid-day (1200-1500 h) for large and medium shrubs on the seeded site through the 1990 growing season.

PRE-DAWN:

Date	Medium	Large	Difference	LSD	
May 31	-1.28	-1.31	+ .03	.13	NS
June 14	-2.12	-1.97	+ .15	.28	NS
June 28	-2.62	-2.33	+ .29	.33	NS
July 12	-3.11	-2.76	+ .35	.53	NS
July 26	-3.72	-3.26	+ .48	.88	NS
August 29	-1.60	-1.77	- .17	.16	*

MID-DAY:

Date	Medium	Large	Difference	LSD	
May 31	-1.75	-1.76	+ .01	.20	NS
June 14	-3.04	-2.96	+ .08	.22	NS
June 28	-3.50	-3.30	+ .20	.34	NS
July 12	-4.36	-4.08	+ .28	.59	NS
July 26	-4.53	-4.15	+ .38	.69	NS
August 29	-2.66	-2.80	- .14	.28	NS

*: Significant difference at $P \leq .10$ between shrub size at that date; NS: Not significantly different at that date.

Table 3. Plant water potential (MPa) at pre-dawn (0400-0500 h) and mid-day (1200-1500 h) for large and medium shrubs on the native site through the 1989 growing season.

PRE-DAWN:

Date	Medium	Large	Difference	LSD	
June 1	- .72	- .70	+ .02	.07	NS
June 12	- .92	- .97	- .05	.12	NS
June 28	-1.01	-1.08	- .07	.15	NS
July 14	-1.31	-1.37	- .06	.14	NS
July 29	-1.88	-1.77	+ .11	.34	NS
August 31	-1.60	-1.72	- .12	.14	NS

MID-DAY:

Date	Medium	Large	Difference	LSD	
June 1	-1.70	-1.68	+ .02	.13	NS
June 12	-1.97	-2.23	- .28	.15	*
June 28	-1.81	-1.98	- .16	.11	*
July 14	-2.66	-2.62	+ .04	.15	NS
July 29	-3.20	-3.09	+ .11	.59	NS
August 31	-2.80	-2.76	+ .05	.33	NS

*: Significant difference at $P \leq .10$ between shrub size at that date; NS: Not significantly different at that date.

Table 4. Plant water potential (MPa) at pre-dawn (0400-0500 h) and mid-day (1200-1500 h) for large and medium shrubs on the native site through the 1990 growing season.

PRE-DAWN:

Date	Medium	Large	Difference	LSD	
May 31	-1.33	-1.59	- .26	.15	*
June 14	-2.22	-1.90	+ .32	.28	*
June 28	-2.71	-2.60	+ .11	.31	NS
July 12	-3.22	-2.84	+ .38	.51	NS
July 26	-3.89	-3.82	+ .07	.57	NS
August 29	-1.75	-1.83	- .08	.21	NS

MID-DAY:

Date	Medium	Large	Difference	LSD	
May 31	-1.86	-2.15	- .29	.23	*
June 14	-3.20	-3.16	+ .04	.30	NS
June 28	-3.64	-3.78	- .14	.35	NS
July 12	-4.18	-4.15	+ .03	.43	NS
July 26	-4.99	-4.77	+ .22	.61	NS
August 29	-3.00	-3.18	- .18	.25	NS

*: Significant difference at $P \leq .10$ between shrub size at that date; NS: Not significantly different at that date.

Table 5. Leaf conductance (g $cm^{-1} sec^{-1}$) at morning (0730-0900 h) and afternoon (1200-1500 h) for medium and large shrubs on the seeded site through the 1989 growing season.

MORNING:

Date	Medium	Large	Difference	LSD	
June 1	.52	.51	- .01	.13	NS
June 12	.58	.50	- .08	.12	NS
June 28	.49	.39	- .10	.12	NS
July 14	.47	.32	- .15	.12	*
July 29	.35	.27	- .08	.10	NS
August 31	.46	.39	- .07	.08	NS

AFTERNOON:

Date	Medium	Large	Difference	LSD	
June 1	.41	.43	+ .02	.10	NS
June 12	.43	.41	- .02	.13	NS
June 28	.33	.25	+ .08	.08	*
July 14	.30	.20	- .10	.09	*
July 29	.17	.14	- .03	.03	*
August 31	.39	.27	- .12	.09	*

*: Significant difference at $P \leq .10$ between shrub size at that date; NS: Not significantly different at that date.

Table 6. Leaf conductance (g $cm^{-1} sec^{-1}$) at morning (0730-0900 h) and afternoon (1200-1500 h) for medium and large shrubs on the seeded site through the 1990 growing season.

MORNING:

Date	Medium	Large	Difference	LSD	
June 14	.16	.21	+ .05	.04	*
June 28	.12	.13	+ .01	.05	NS
July 12	.15	.10	- .05	.06	NS
July 26	.15	.15	0	.05	NS
August 29	.26	.20	- .06	.06	*

AFTERNOON:

Date	Medium	Large	Difference	LSD	
June 14	.09	.13	+ .04	.03	*
June 28	.04	.05	+ .01	.02	NS
July 12	.07	.05	- .02	.03	NS
July 26	.10	.11	+ .01	.03	NS
August 29	.21	.17	- .04	.03	*

*: Significant difference at $P \leq .10$ between shrub size at that date; NS: Not significantly different at that date.

Table 7. Leaf conductance (g $cm^{-1} sec^{-1}$) at morning (0730-0900 h) and afternoon (1200-1500 h) for medium and large shrubs on the native site through the 1989 growing season.

MORNING:

Date	Medium	Large	Difference	LSD	
June 1	.58	.58	0	.14	NS
June 12	.60	.47	- .13	.11	*
June 28	.54	.42	- .12	.09	*
July 14	.43	.34	- .09	.08	*
July 29	.33	.37	+ .04	.12	NS
August 31	.29	.27	- .02	.06	NS

AFTERNOON:

Date	Medium	Large	Difference	LSD	
June 1	.42	.41	- .01	.09	NS
June 12	.49	.40	- .09	.12	NS
June 28	.55	.31	- .24	.30	NS
July 14	.28	.20	- .08	.07	*
July 29	.25	.23	- .02	.07	NS
August 31	.33	.22	- .11	.10	*

*: Significant difference at $P \leq .10$ between shrub size at that date; NS: Not significantly different at that date.

Table 8. Leaf conductance (g $cm^{-1} sec^{-1}$) at morning (0730-0900 h) and afternoon (1200-1500 h) for medium and large shrubs on the native site through the 1990 growing season.

MORNING:

Date	Medium	Large	Difference	LSD	
June 14	.26	.25	- .01	.06	NS
June 28	.11	.10	- .01	.03	NS
July 12	.10	.13	+ .03	.05	NS
July 26	.13	.14	+ .01	.06	NS
August 29	.37	.28	- .09	.09	*

AFTERNOON:

Date	Medium	Large	Difference	LSD	
June 14	.11	.10	- .01	.04	NS
June 28	.03	.03	0	.01	NS
July 12	.06	.07	+ .01	.02	NS
July 26	.07	.06	- .01	.03	NS
August 29	.28	.26	- .02	.10	NS

*: Significant difference at $P \leq .10$ between shrub size at that date; NS: Not significantly different at that date.

Shrub Growth:

Shrub Size Effect: The proportion of vegetative and reproductive stems and leaf types was different between medium and large shrubs (Tables 9 and 10).

Large shrubs had 39% and 31% fewer perennial leaves per vegetative shoot and per unit length of vegetative shoot, respectively, compared to medium shrubs in 1989 on the seeded site. However, large shrubs had significantly more leaves per unit of reproductive shoot length than medium shrubs on the seeded site in 1989 and on both sites in 1990. Medium shrubs had at most only 11% the number of leaves that large shrubs had on reproductive stems per unit area of canopy.

Vegetative shoots were 31% longer on medium shrubs than large shrubs on the native site in 1990. Lateral stem lengths on large shrubs were 30% shorter than on medium shrubs in 1989 on the seeded site. There were no lateral stems present on shrubs on the native site in 1990. Reproductive shoot lengths, however, were greater for large shrubs on both sites in both years, compared to medium shrubs.

Leaf dry weight per reproductive shoot was greater for large shrubs than medium shrubs in 1989 on the native site and on both sites in 1990. Large shrubs also had significantly greater biomass per reproductive stem in 1989 and 1990 on the seeded site and in 1990 on the native site,

and greater biomass per reproductive shoot in 1989 and 1990 on the seeded site, compared to medium shrubs. Reproductive stem weight was greater for large shrubs than medium shrubs per unit area of canopy in 1989 and 1990 on the seeded site. Reproductive shoot weight per unit area of canopy was significantly greater (540%) for large shrubs than medium shrubs on the seeded site in 1990. Vegetative stem weight was 38% greater for medium shrubs than for large shrubs in 1990 on the seeded site.

Treatment Effect: Defoliation treatment changed the proportional development of vegetative and reproductive stems and leaf types (Tables 11 and 12).

Vegetative stems in defoliated plots were 7% shorter, and reproductive stems weighed 8% less per unit area of canopy than shrubs on control plots in 1989 on the seeded site. In 1990 on the seeded site, shrubs in defoliated plots had 18% more perennial leaves per unit of vegetative shoot length, 12% fewer primary ephemeral leaves per shoot, and 11% fewer ephemeral leaves total (primary and secondary) per shoot compared to shrubs on the undefoliated plots. On the native site in 1990, the mean number of ephemeral leaves per shoot was 8% higher for shrubs in defoliated plots.

Table 9. Growth response of medium and large shrubs in 1989.

Variable	Seeded Site		Native Site	
	Medium	Large	Medium	Large
Leaves				
Annual leaves (lvs)/meter (m) vegetative (veg) shoot	1,116	775 *	1,024	992
Annual lvs/m reproductive (repro) shoot	767	645	67	722 *
Annual lvs/veg. shoot	110	69 *	40	47
Annual lvs/repro. shoot	110	179 *	17	67 *
Annual lvs on repro. shoots/m^2 canopy	7,629	86,156 *	1,129	11,766 *
Primary ephemeral lvs/m veg. shoot	112	122	265	389
Primary ephemeral lvs/veg. shoot	10.8	10.9	9.0	8.6
Secondary ephemeral lvs/m veg. shoot	120.3	104.2	115.6	68.0
Secondary ephemeral lvs/veg. shoot	11.9	9.8	5.9	4.4
Ephemeral lvs (total)/veg. shoot	22.7	20.7	14.9	12.9
Dry weight (wt) lvs/veg. shoot (mg)	336	305	97	138
Dry wt lvs/repro. shoot (mg)	141	232	22	89 *
Dry wt lvs on repro. shoots/m^2 canopy	7,162	109,610 *	1,231	16,030 *t
Stems				
Length (mm)/veg. stem	100	91	41	48
Length (mm)/repro. stem	204	271 *	21	99 *
Dry wt/veg. stem	132	101	29	38
Dry wt/repro. stem	282	465 *	19	91 *t
Dry wt of repro. stems/m^2 canopy	17,301	215,648 *	1,345	15,140 *t
Length/lateral stem	9.3	6.5 *	2.5	3.2
Length of laterals/veg. shoot	64.4	32.5 *t	5.8	5.5
Shoots				
Dry wt/veg. shoot	493	418	128	178
Dry wt/repro. shoot	405	697 *	41	179 *t
Dry wt of repro. shoots/m^2 canopy	25,753	330,721 *t	2,576	31,273 *t

*: significantly different between sizes on that site at $P \leq .10$; t: significant interaction between treatment and size on that site.

Table 10. Growth response of medium and large shrubs in 1990.

Variable	Seeded Site			Native Site		
	Medium	Large		Medium	Large	
Leaves						
Annual leaves (lvs)/meter (m) vegetative (veg) shoot	1,850	1,977	*	1,612	1,775	
Annual lvs/m reproductive (repro) shoot	365	977	*	0	702	*
Annual lvs/veg. shoot	30	30		23	20	
Annual lvs/repro. shoot	26	48	*	5	24	*
Annual lvs on repro. shoots/m^2 canopy	2,938	16,634	*	0	2,212	*
Primary ephemeral lvs/m veg. shoot	388	413	*	389	474	
Primary ephemeral lvs/veg. shoot	6.1	6.0		5.2	4.9	
Secondary ephemeral lvs/m veg. shoot	3.9	14.2		4.5	8.2	
Secondary ephemeral lvs/veg. shoot	0.1	0.2		0.1	0.1	
Ephemeral lvs (total)/veg. shoot	6.2	6.1		5.3	5.0	
Dry weight (wt) lvs/veg. shoot (mg)	74	84		41	42	
Dry wt lvs/repro. shoot (mg)	27	50	*	3	24	*
Dry wt lvs on repro. shoots/m^2 canopy	2,972	17,256	*	0	2,194	*
Stems						
Length/veg. stem (mm)	17	15		15	11	*
Length/repro. stem (mm)	40	77	*	6	31	*
Dry wt/veg. stem (mg)	14	10	*	8	7	
Dry wt/repro. stem (mg)	23	54	*	3	18	*
Dry wt of repro. stems/m^2 canopy (mg)	2,642	18,644	*	0	1,774	
Length/lateral stem (mm)	0	0.3		0	0	
Length of laterals/veg. shoot (mm)	0	0.1		0	0	
Shoots						
Dry wt/veg. shoot (mg)	88.0	94.0		49.0	49.0	
Dry wt/repro. shoot (mg)	50.0	104.0	*	6.0	42.0	*t
Dry wt of repro. shoots/m^2 canopy (mg)	5,613.0	35,900.0	*	0	3,968.0	

*: significantly different between sizes on that site at $P \leq .10$; t: significant interaction between treatment and size on that site.

Table 11. Treatment effect on shrub growth response in 1989.

Variable	Seeded Site		Native Site	
	Control	Defoliated	Control	Defoliated
Leaves				
Annual leaves (lvs)/meter (m) vegetative (veg) shoot	933.8	957.9	992.5	1,023.6
Annual lvs/m reproductive (repro) shoot	626.5	784.9	378.4	410.6
Annual lvs/veg. shoot	91.3	87.7	46.0	40.5
Annual lvs/repro. shoot	140.5	148.3	43.2	41.0
Annual lvs on repro. shoots/m^2 canopy	49,346.0	44,439.0	5,415.0	7,480.0
Primary ephemeral lvs/m veg. shoot	115.6	117.7	212.5	245.7
Primary ephemeral lvs/veg. shoot	11.0	10.8	9.2	8.3
Secondary ephemeral lvs/m veg. shoot	108.9	115.6	100.0	83.7
Secondary ephemeral lvs/veg. shoot	10.8	10.9	5.4	4.9
Ephemeral lvs (total)/veg. shoot	21.8	21.6	14.6	13.2
Dry weight (wt) lvs/veg. shoot (mg)	330.2	311.3	120.5	114.4
Dry wt lvs/repro. shoot (mg)	172.5	201.0	54.7	55.8
Dry wt lvs on repro. shoots/m^2 canopy	60,306.0	56,467.0	6,847.0	10,414.0
Stems				
Length (mm)/veg. stem	99.1	92.5 *	47.2	41.8
Length (mm)/repro. stem	244.6	230.9	64.8	55.4
Dry wt/veg. stem (mg)	122.4	110.4	36.2	30.7
Dry wt/repro. stem (mg)	371.1	375.5	55.8	55.9
Dry wt of repro. stems/m^2 canopy (mg)	121,369.0	111,581.0 *	7,378.0	92.0
Length/lateral stem (mm)	7.9	7.8	3.2	2.4
Length of laterals/veg. shoot (mm)	53.1	43.8	5.6	5.6
Shoots				
Dry wt/veg. shoot (mg)	473.0	438.0	158.0	147.0
Dry wt/repro. shoot (mg)	544.0	558.0	109.0	112.0
Dry wt of repro. shoots/m^2 canopy (mg)	185,129.0	171,344.0	14,252.0	19,596.0

*: significantly different between sizes on that site at $P \leq .10$.

Table 12. Treatment effect on shrub growth response in 1990.

Variable	Seeded Site		Native Site	
	Control	Defoliated	Control	Defoliated
Leaves				
Annual leaves (lvs)/meter (m) vegetative (veg) shoot	1,753	2,074 *	1,578	1,809
Annual lvs/m reproductive (repro) shoot	722.4	619.9	314.3	387.3
Annual lvs/veg. shoot	30.9	29.4	20.3	22.2
Annual lvs/repro. shoot	37.3	36.9	12.9	16
Annual lvs on repro. shoots/m^2 canopy	8,902	10,670	993	1,220
Primary ephemeral lvs/m veg. shoot	396.9	403.5	413.3	449.8
Primary ephemeral lvs/veg. shoot	6.4	5.6 *	4.9	5.2
Secondary ephemeral lvs/m veg. shoot	5.2	12.9	1.7	11.0
Secondary ephemeral lvs/veg. shoot	.105	.150	.020	.180
Ephemeral lvs (total)/veg. shoot	6.5	5.8 *	5.0	5.4 *
Dry weight (wt) lvs/veg. shoot (mg)	82.7	76	40.2	42.4
Dry wt lvs/repro. shoot (mg)	40.6	36.5	11.1	16.2
Dry wt lvs on repro. shoots/m^2 canopy	9,890	10,338	950	1,243
Stems				
Length (mm)/veg. stem	17.8	14.8	12.9	13.2
Length (mm)/repro. stem	58.4	58.8	17.4	19.4
Dry wt/veg. stem	13.7	10.1	7.8	7.5
Dry wt/repro. stem	37.6	39.1	8.4	12.3
Dry wt of repro. stems/m^2 canopy	9,987	11,299	685	1,089
Length/lateral stem	0	.30	0	0
Length of laterals/veg. shoot	0	.06	0	0
Shoots				
Dry wt/veg. shoot	96.4	86.1	48.0	49.9
Dry wt/repro. shoot	78.2	75.6	19.7	28.5
Dry wt of repro. shoots/m^2 canopy	19,877.0	21,637.0	1,635.0	2,333.0

*: significantly different between sizes on that site at $P \leq .10$.

Nitrogen Content: Nitrogen content was 11% greater in foliage from shrubs in control plots than in defoliated plots in 1989 on the native site (Table 13, Figure 4). No other significant differences in nitrogen content were detected between treatment or shrub size combinations in either year.

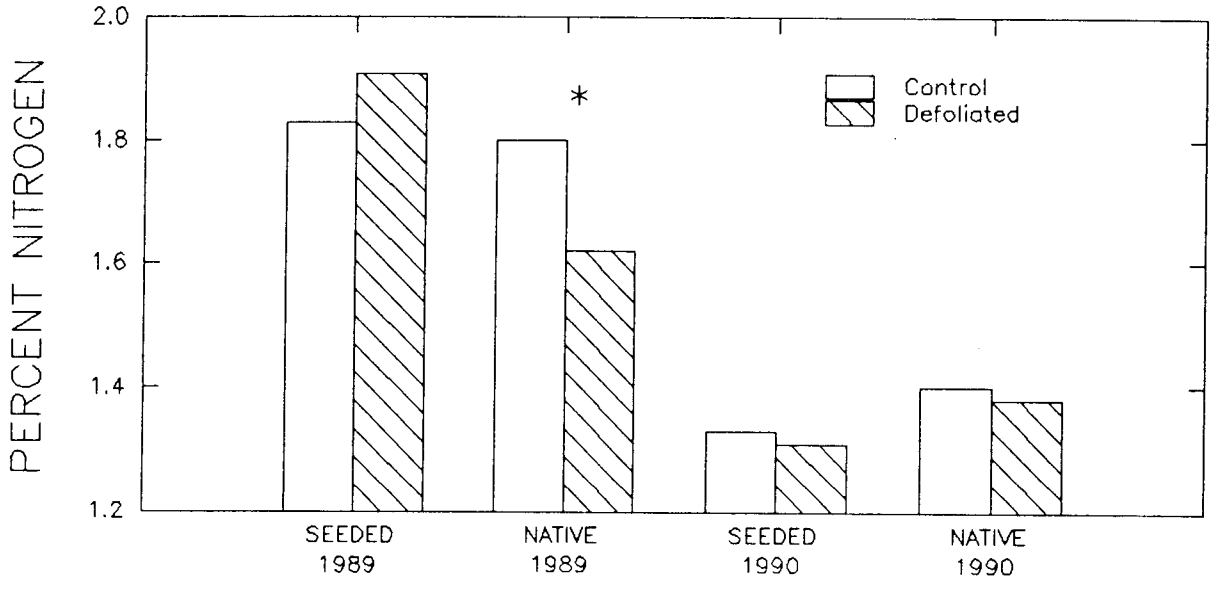


Figure 4. Percent nitrogen in current year's growth for control and defoliated plots. Significance at $P \leq .10$.

Table 13. Leaf nitrogen content (ppm) for control and defoliated treatments in 1989 and 1990.

1989

Site	Control	Defoliated	Critical Difference	
Seeded	18,300	19,100	2,000	NS
Native	18,000	16,200	1,800	*

1990

Site	Control	Defoliated	Critical Difference	
Seeded	13,300	13,100	2,100	NS
Native	14,000	13,800	400	NS

*: Significantly different between treatments on that site at $P \leq .10$; NS: Not significantly different between sizes on that site; Values are means of 10 samples per treatment in 1989 and in 1990.

II. Defoliation Study -- Seedling Plots:

Soil Moisture: Soil moisture content did not differ significantly between control and defoliated seedling plots.

Seedling Survival: Percent survival data for seedling plots is shown in Table 14. By the end of the 1990 season, only 8.5% of seedlings in control plots and 22.7% of seedlings in defoliated plots were still alive. Survival rate was not significantly different between control and defoliated plots on any date. Recruitment of new seedlings did not occur during the study period.

It appeared that seedling density had no effect on survival of seedlings, at least in plots with seedling densities under 150. However, once densities exceeded 150, seedling survival appeared to be negatively affected by increasing density.

Table 14. Percent survival of sagebrush seedlings from initial date (June 19, 1989).

Date	Control	Defoliated
July 1, 1989	95 %	92 %
July 17, 1989	72 %	75 %
August 1, 1989	50 %	59 %
August 15, 1989	41 %	52 %
August 27, 1989	37 %	47 %
March 19, 1990	31 %	46 %
May 12, 1990	29 %	46 %
June 13, 1990	29 %	45 %
June 28, 1990	27 %	43 %
July 11, 1990	23 %	41 %
July 26, 1990	19 %	37 %
August 17, 1990	9 %	24 %
August 28, 1990	9 %	23 %

III. Drought Study:

Environmental:

Weather: As discussed in the defoliation study above and shown in Figures 2 and 3.

Soil Moisture: Differences in percent soil moisture between 1989 and 1990 were significant on both the seeded and native sites (Table 15, Figures 5 and 6). On the native site there was a significant interaction between year and date. Soil moisture was greater on most dates in 1989 compared to 1990 in both the 20-200 and 200-400 mm soil profiles. Differences between years were less pronounced as the season progressed.

Plant Water Relations:

Plant Water Potential: Pre-dawn and mid-day plant water potentials were significantly higher (plants were less water-stressed) in 1989 than in 1990 on all dates, for both sites (Figures 7, 8, 9 and 10). Differences in plant water potentials between years were greatest from the early July to early August dates. Differences were less pronounced on the early June and late August sampling dates.

Leaf Conductance: Morning and afternoon leaf conductance of sagebrush were significantly higher in 1989 than in 1990 on all but one date (Figures 12, 13, 14 and 15). The only exception was afternoon conductance on the

September 1 date on the native site, where there was no difference between years. Conductance declined through mid to late August in 1989 before increasing; conductance decreased until mid-July before increasing.

Table 15. Percent soil moisture content in the 2-20 cm soil depth through the 1989 and 1990 growing seasons.

SEEDED SITE:

Date	1989	1990	Difference	LSD	
Early June	11.50	8.62	- 2.88	1.14	*
Mid June	8.94	6.10	- 2.84	.52	*
Late June	7.45	5.29	- 2.16	.39	*
Mid July	6.21	4.99	- 1.22	.44	*
Late July	4.21	4.11	- .10	.38	NS
Late August	--	5.00			

NATIVE SITE:

Date	1989	1990	Difference	LSD	
Early June	10.91	8.66	- 2.25	.78	*
Mid June	7.59	5.39	- 2.20	.56	*
Late June	5.71	4.61	- 1.10	.55	*
Mid July	5.01	4.64	- .37	.39	NS
Late July	3.03	3.96	+ .93	.36	*
Late August	--	4.81			

*: Significant difference at $P \leq .10$ between years at that date; NS: Not significantly different at that date.

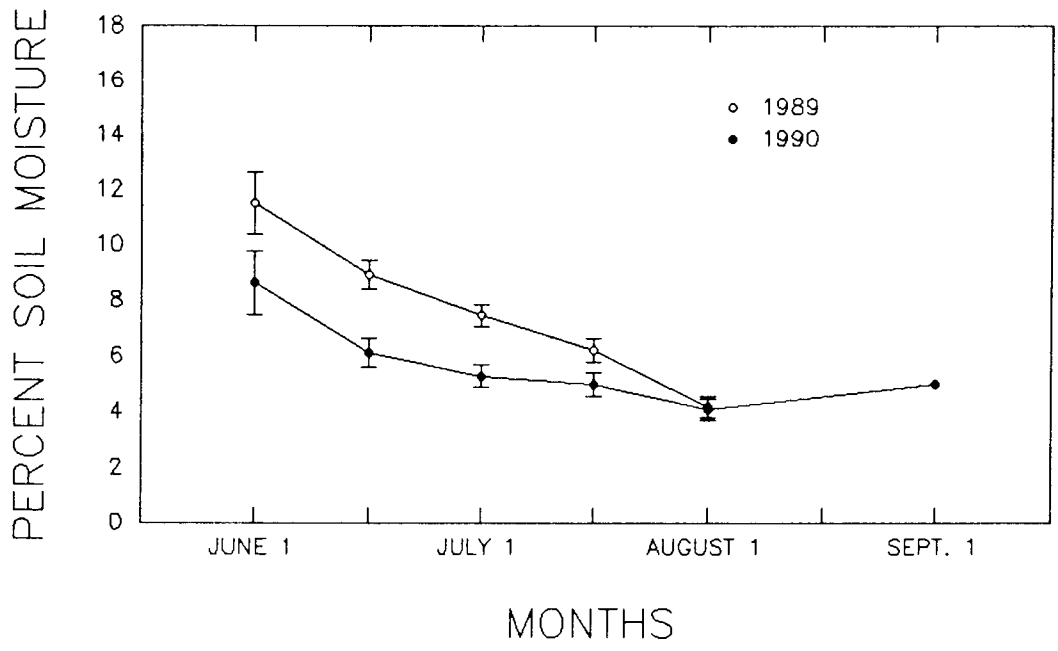


Figure 5. Seasonal pattern of soil moisture content in the upper (20-200 mm) soil profile for the seeded site in 1989 and 1990. Field capacity is 23% soil moisture, wilting point is 9% soil moisture content.

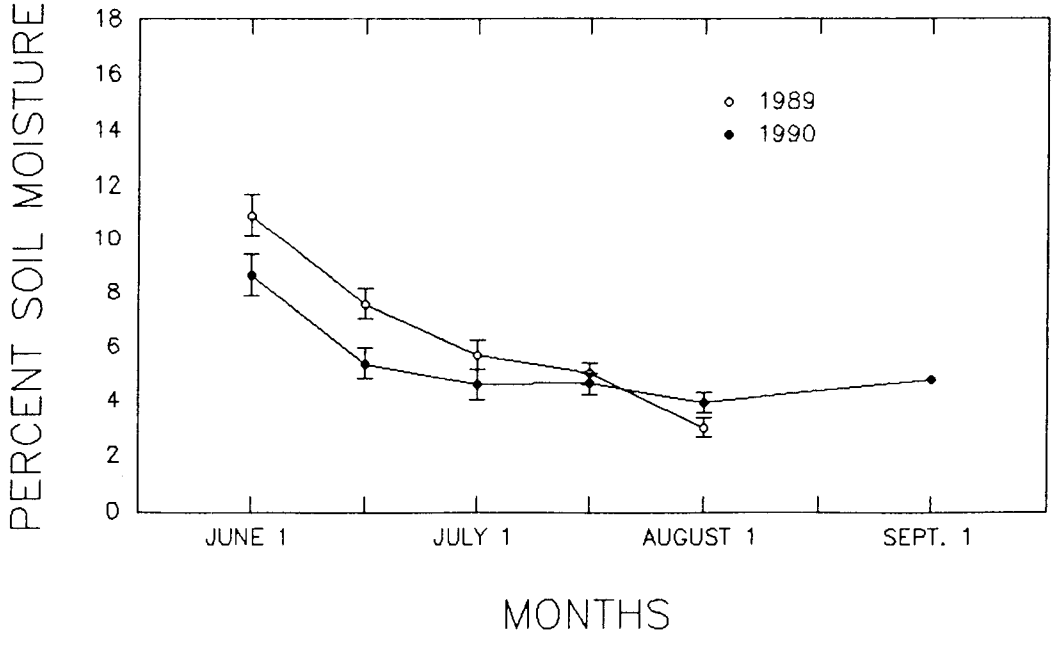


Figure 6. Seasonal pattern of soil moisture content in the upper (20-200 mm) soil profile for the native site in 1989 and 1990. Field capacity is 23% soil moisture, wilting point is 9% soil moisture content.

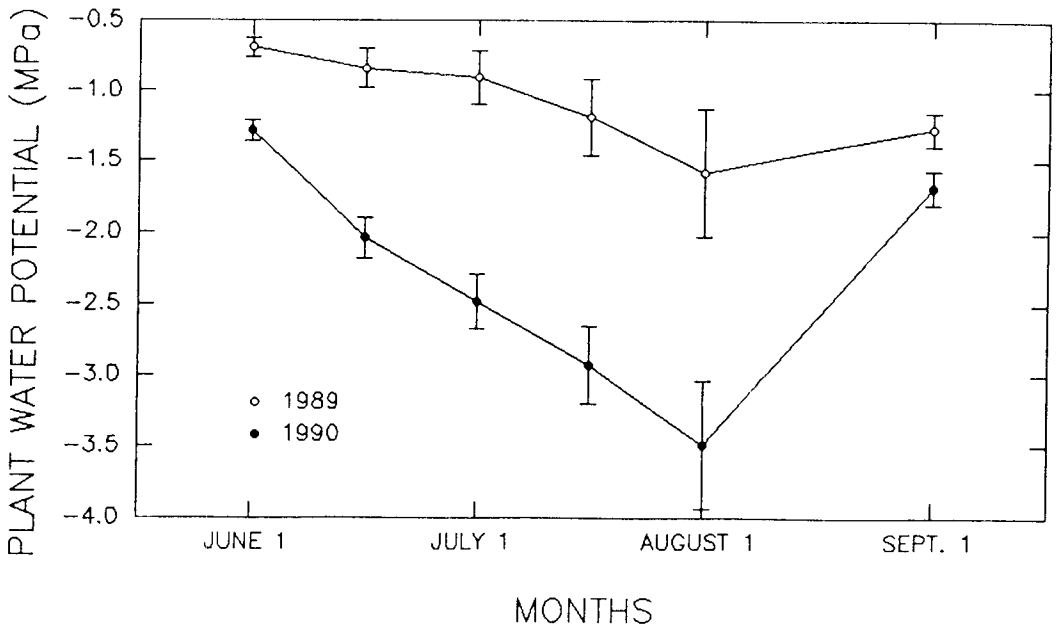


Figure 7. Plant water potential at predawn (0400-0500 h) on the seeded site in 1989 and 1990.

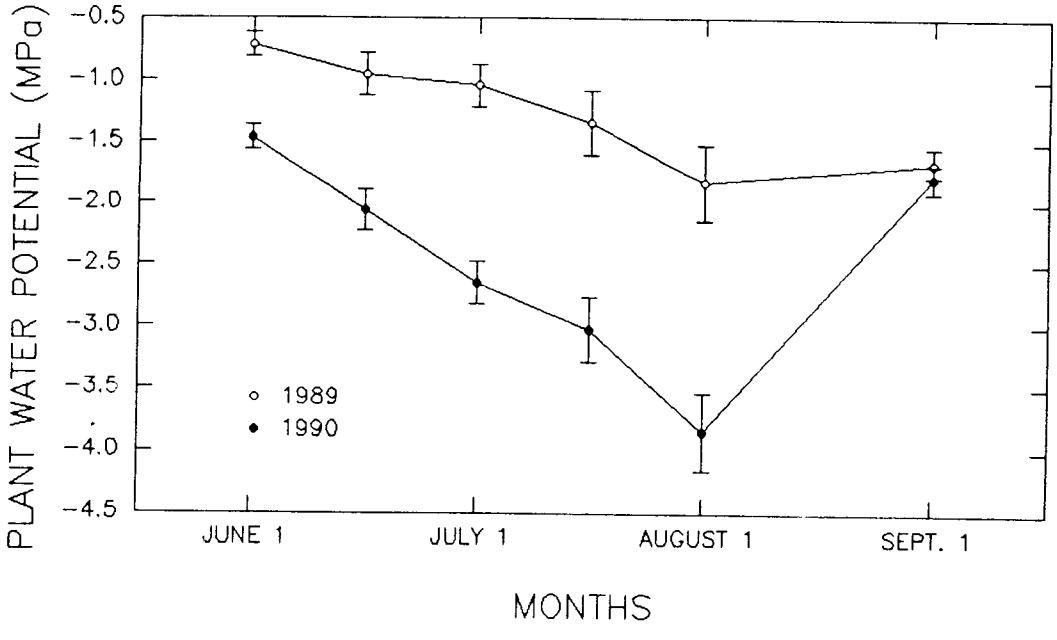


Figure 8. Plant water potential at predawn (0400-0500 h) on the native site in 1989 and 1990.

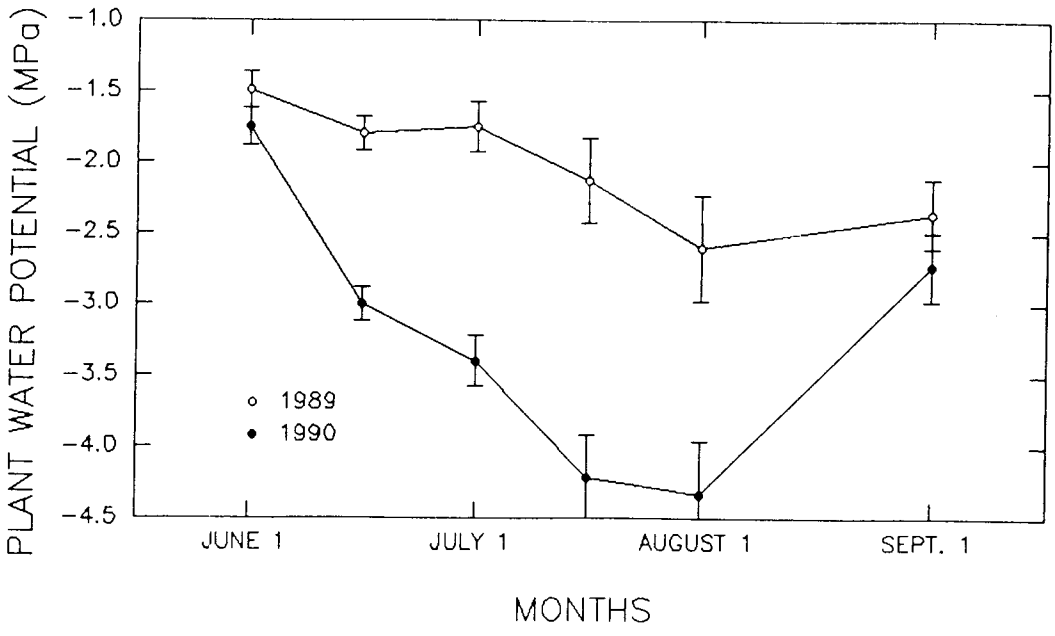


Figure 9. Plant water potential at mid-day (1200-1500 h) on the seeded site in 1989 and 1990.

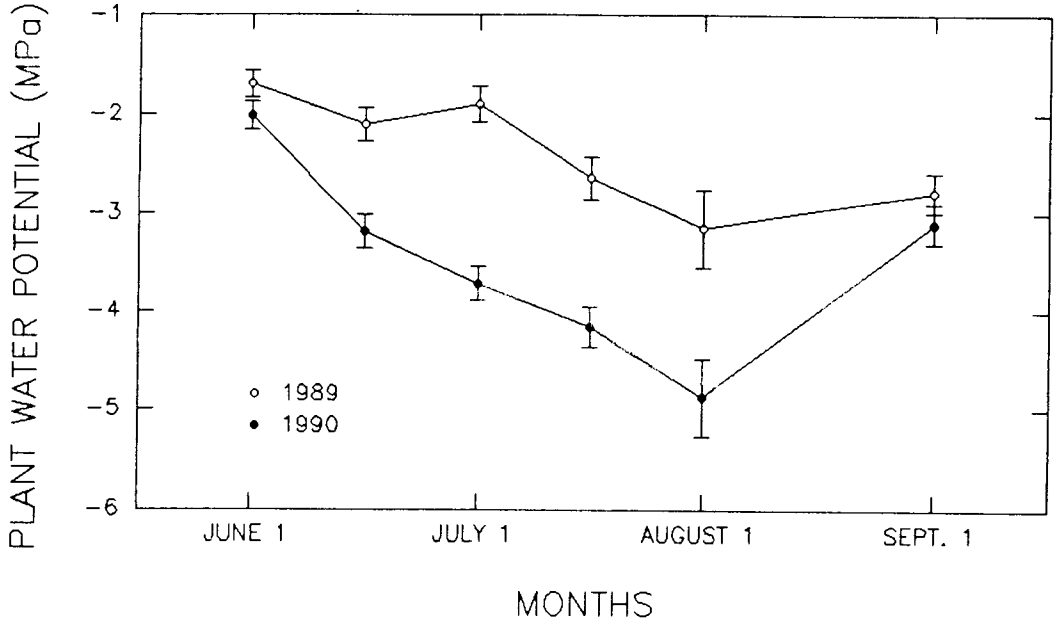


Figure 10. Plant water potential at mid-day (1200-1500 h) on the native site in 1989 and 1990.

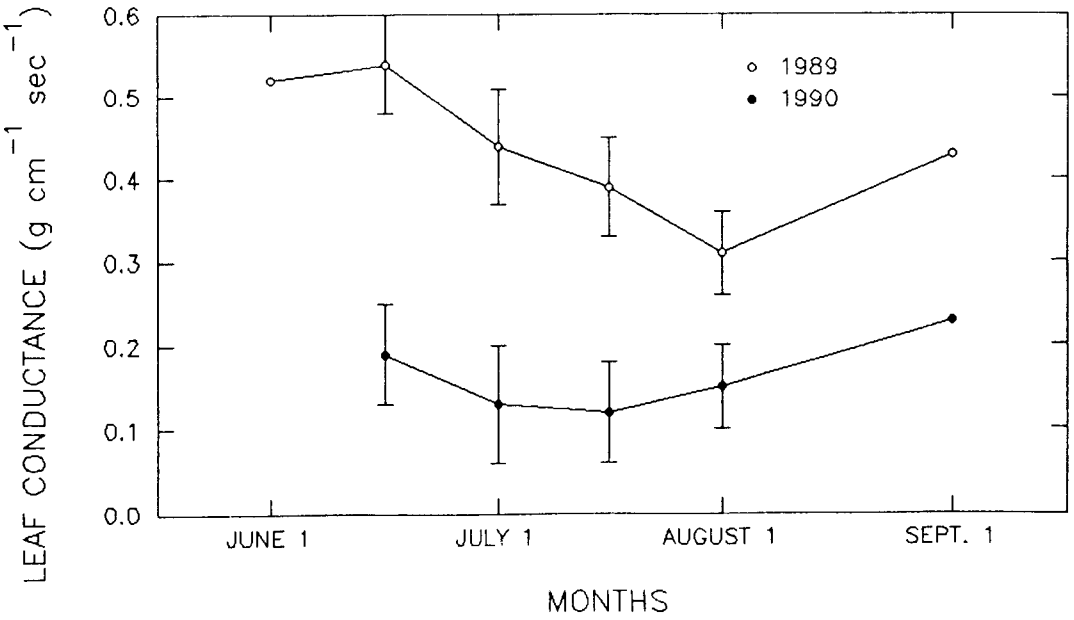


Figure 11. Leaf conductance (g $cm^{-1}sec^{-1}$) in the morning (0730-0900 h) on the seeded site in 1989 and 1990.

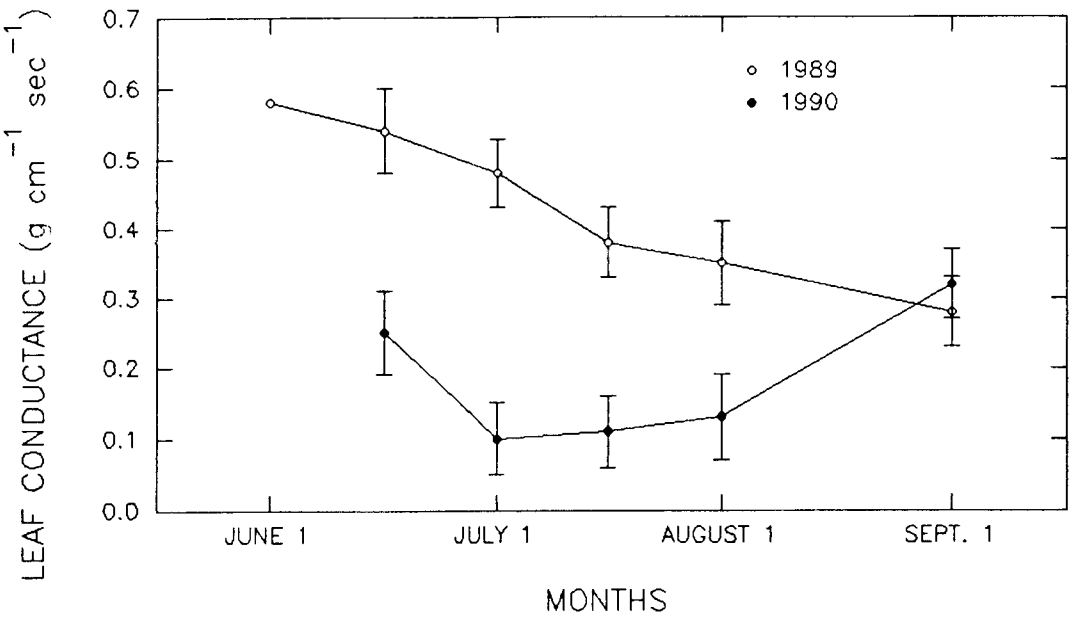


Figure 12. Leaf conductance (g $cm^{-1}sec^{-1}$) in the morning (0730-0900 h) on the native site in 1989 and 1990.

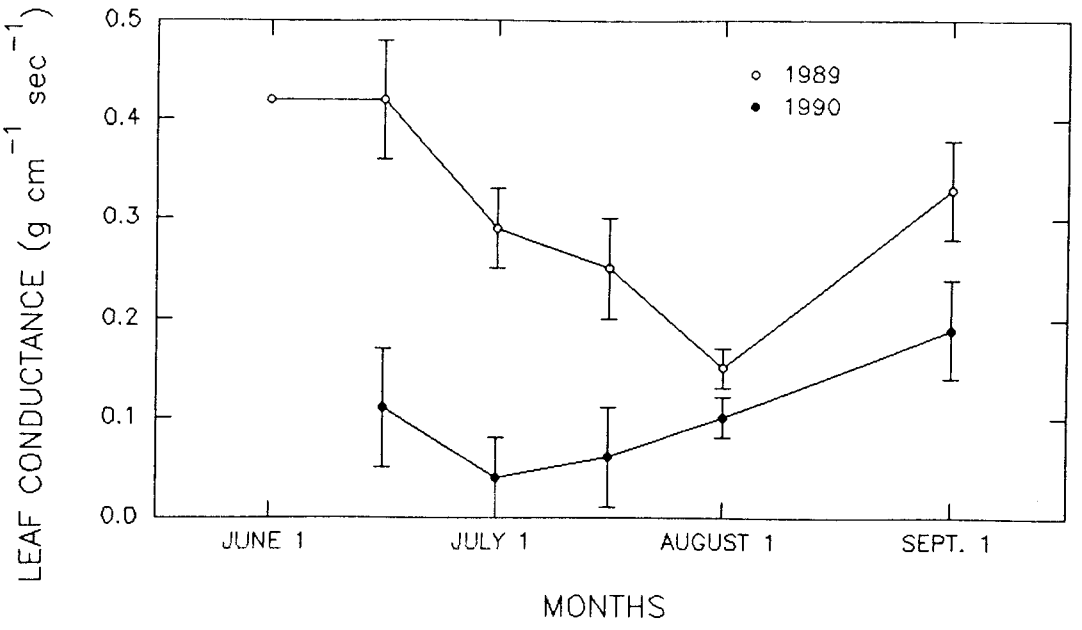


Figure 13. Leaf conductance (g cm^{-1}sec^{-1}) in the afternoon (1200-1500 h) on the seeded site in 1989 and 1990.

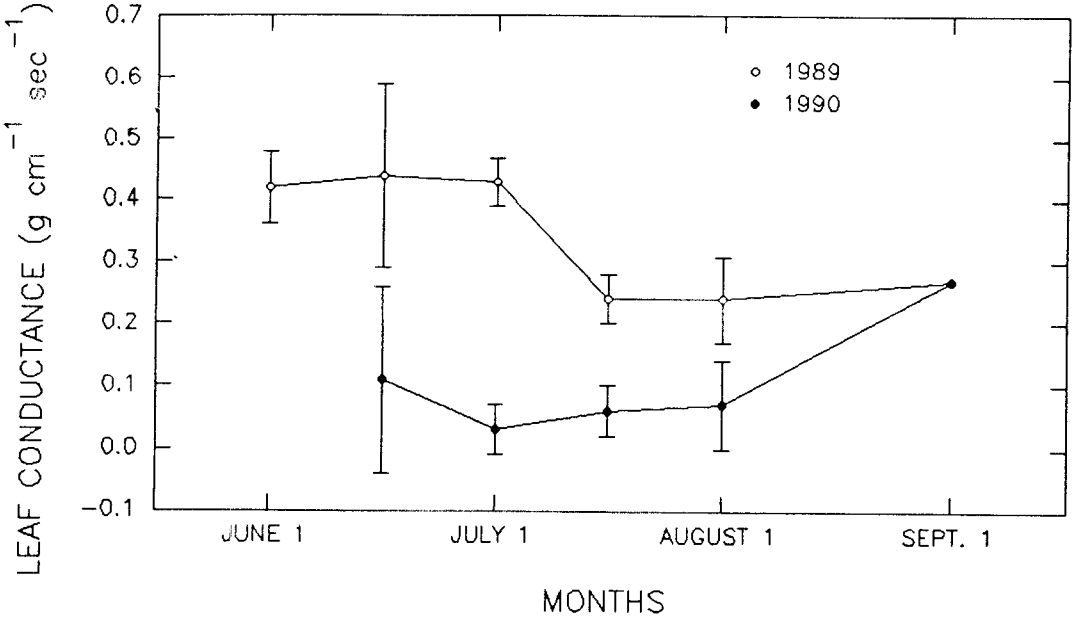


Figure 14. Leaf conductance (g cm^{-1}sec^{-1}) in the afternoon (1200-1500 h) on the native site in 1989 and 1990.

Shrub Growth: The relative drought of 1990 resulted in significantly less aboveground biomass production compared to 1989 (Tables 16 and 17). Mean individual vegetative shoot (stem plus leaves) weight was 80 and 68% less in 1990 compared to 1989 on the seeded and native sites, respectively. Mean individual reproductive shoot weight was 86 and 78% less in 1990 compared to 1989 on the seeded and native sites, respectively. In 1989, mean vegetative shoot weight was less than mean reproductive shoot weight on the seeded site but more than mean reproductive shoot weight on the native site. In 1990, mean individual vegetative shoots weighed more than reproductive shoots on both sites.

The proportion of different leaf types changed between the two years. In the drought year, fewer annual and primary ephemeral leaves developed on both sites. However, in the drought year, the proportional decrease in ephemeral leaves was greater than the decrease in annual leaves. For example, on the seeded site in the drought year the number of ephemeral leaves decreased by 92%, compared to only 66% for annual leaves.

The drought also produced significant changes in the proportion of vegetative versus reproductive growth. In the drought year, there was a proportionally greater reduction in weight and number of reproductive versus vegetative leaves on the seeded site. The trend was similar for vegetative and reproductive stems.

In the drought year compared to the previous growing season, there was a greater reduction in stem development than in leaf development of reproductive shoots. For example, on the seeded site leaf weight per reproductive shoot decreased only 79%, compared to a 90% reduction in weight of stem per reproductive shoot. Vegetative stems and leaves responded in the same manner as reproductive stems and leaves to the drought.

Table 16. Shrub growth on the seeded site for 1989 and 1990.

SEEDED SITE:

Variable:	1989	1990	% Change:	
Leaves:				
Annual leaves (lvs)/meter (m) vegetative (veg) shoot	946	1,913	+102%	*s
Annual lvs/veg. shoot	89	30	- 66%	*
Dry wt (mg) annual lvs/veg. shoot	321	79	- 75%	*
Primary ephemeral lvs/veg. shoot	11	6	- 45%	*
Primary ephemeral lvs/m veg. shoot	117	400	+242%	*
Secondary ephemeral lvs/veg. shoot	11	0	-100%	
Secondary ephemeral lvs/m veg. shoot	112	9	- 92%	*
Ephemeral lvs (total)/veg. shoot	22	6	- 73%	*
Lvs/m reproductive (repro) shoot	706	671	- 5%	
Lvs/repro. shoot	144	37	- 74%	*
Lvs on repro. stems/m^2 canopy	46,892	9,786	- 79%	*s
Dry wt (mg) lvs/repro. shoot	187	39	- 79%	*
Dry wt (mg) lvs on repro. shoots/m^2 canopy	58,386	10,114	- 83%	*s
Stems:				
Length (mm)/veg. stem	96	16	- 83%	*
Dry wt (mg)/veg. stem	116	12	- 90%	*
Length (mm)/repro. stem	238	59	- 75%	*
Dry wt (mg)/repro. stem	373	38	- 90%	*
Dry wt of repro. stems/m^2 canopy	116,475	10,643	- 91%	*s
Length (mm)/lateral stem	79	2	- 97%	*
Length (mm) of laterals/veg. shoot	485	0	-100%	
Shoots:				
Dry wt (mg)/veg. shoot	455	91	- 80%	*
Dry wt (mg)/repro. shoot	551	77	- 86%	*
Dry wt (mg) repro. shoots/m^2 canopy	178,237	20,757	- 88%	*s

*: Significantly different between years at $P \leq .10$; s: significant interaction at $P \leq .10$ between year and size; t: significant interaction at $P \leq .10$ between year and treatment.

Table 17. Shrub growth on the native site for 1989 and 1990.

NATIVE SITE:

Variable:	1989	1990	% Change:	
Leaves:				
Annual leaves (lvs)/meter (m) vegetative (veg) shoot	1,008	1,694	+ 68%	*ts
Annual lvs/veg. shoot	43	21	- 51%	
Dry wt (mg) annual lvs/veg. shoot	118	41	- 65%	
Primary ephemeral lvs/veg. shoot	9	5	- 44%	
Primary ephemeral lvs/m veg. shoot	229	431	+ 88%	*
Secondary ephemeral lvs/veg. shoot	5	1	- 80%	
Secondary ephemeral lvs/m veg. shoot	92	6	- 93%	
Ephemeral lvs (total)/veg. shoot	14	5	- 64%	
Lvs/m reproductive (repro) shoot	394	351	- 11%	*ts
Lvs/repro. shoot	42	14	- 67%	
Lvs on repro. stems/m^2 canopy	6,448	1,106	- 83%	
Dry wt (mg) lvs/repro. shoot	55	14	- 75%	
Dry wt (mg) lvs on repro. shoots/m^2 canopy	8,630	1,097	- 87%	
Stems:				
Length (mm)/veg. stem	44	13	- 70%	*
Dry wt (mg)/veg. stem	33	8	- 76%	
Length (mm)/repro. stem	60	18	- 70%	
Dry wt/repro. stem	55	10	- 82%	
Dry wt (mg) repro. stems/m^2 canopy	8,242	887	- 89%	
Length (mm)/lateral stem	28	0	-100%	*
Length (mm) of laterals/veg. shoot	56	0	-100%	
Shoots:				
Dry wt (mg)/veg. shoot	153	49	- 68%	
Dry wt (mg)/repro. shoot	110	24	- 78%	
Dry wt (*mg) repro. shoots/m^2 canopy	16,924	1,984	- 88%	

*: Significantly different between years at $P \leq .10$; s: significant interaction at $P \leq .10$ between year and size; t: significant interaction at $P \leq .10$ between year and treatment.

Nitrogen Content: Nitrogen content in current year's growth was 41% higher on the seeded site and 22% higher on the native site in 1989 compared to 1990 (Table 18).

Table 18. Nitrogen content (ppm) in current year's growth for 1989 and 1990.

	1989	1990	Difference	LSD	
Seeded Site:	18,700	13,300	- 5,400	4,300	*
Native Site:	17,100	14,000	- 3,100	2,700	*

*: Significant difference at $P \leq .10$ between years at that date.

DISCUSSION:

Treatment Effects:

My primary hypothesis was that defoliation of understory grasses would increase soil resources such as moisture and nitrogen to the benefit of associated Artemisia. Thus, the capacity of defoliated plants to absorb soil moisture and nitrogen should decline due to decreased root growth and a decrease in transpirational surface area (Crider 1955, Richards 1984). Increased soil moisture on defoliated plots has been shown in several recent studies (Wraith et al. 1987, Miller et al. 1989, Stuart-Hill and Tainton 1989), but not in the current study. I found no differences in soil moisture content between control and defoliated plots.

An explanation for the lack of difference in soil moisture content between treatments is that defoliation prevents accumulation of plant litter, reducing soil shading and increasing area of soil exposed to sun and wind (Whitman 1971). Evaporation from the soil may therefore have offset a small increase in soil moisture. Another reason for lack of soil moisture response to treatment is that defoliation may have afforded some advantage to the grasses, such as rejuvenating senescent leaves (Hodgkinson 1974), increasing tillering (McNaughton 1983), activating dormant buds (vanOverbeek 1977), improving water status of remaining

leaves (McNaughton et al. 1983), stimulating new growth (Trlica 1977), or improving microclimate and nutrient supply around defoliated plants (Chew 1974, Owen and Weigert 1976). The result may have been such that there was no net decrease in the water uptake of defoliated plants. It is also possible that the amount of grass present in plots was too small to release substantial moisture to benefit associated undefoliated shrubs. Another explanation is that extra soil moisture may have been quickly used by Artemisia. Artemisia has high leaf area and conductance rates in the spring, due to presence of ephemeral leaves (Miller and Shultz 1987). It also has an extensive and efficient root system which can take advantage of pulses of soil moisture recharge (Sturges 1977, Caldwell 1978). These characteristics may have contributed to quick extraction of soil moisture not used by grasses. My method of monitoring soil moisture may not have detected quick changes in soil moisture. However, data do not support this explanation because improved water relations and growth of Artemisia should have been evident. There was no clear indication that this occurred.

An increase in soil moisture should have resulted in less negative mature shrub water relations, increased growth, higher current year's nitrogen content, and enhanced seedling survival. Previous studies of understory defoliation have shown that Artemisia growth increased with selective defoliation (or grazing) of understory vegetation

(Weaver 1930, Laycock 1967, Pendery and Provenza 1987). However, in the present study I found no differences in plant water potential or leaf conductance between control and defoliated plots, and only a scattering of contrasting differences in shrub growth responses. The lack of response in plant water potential was consistent with research by Branson et al. (1976).

Shrub seedling response further supports that no change in soil moisture and no subsequent change in plant health resulted from defoliation treatment. Some researchers have detected differences in seedling survival between defoliated and undefoliated areas. In those cases, Artemisia seedling density increased on grazed versus ungrazed areas (Hubbard 1957). Pechanec (1954) also found that grazing increased reinvasion by Artemisia. The results of my study were consistent with the findings of Reed and Peterson (1961), who found seedlings on undefoliated plots experienced similar mortality to those on defoliated plots.

Nitrogen content in current year's growth did not respond as expected to the defoliation treatment. I assumed that defoliation of grasses would decrease understory acquisition of soil resources (including nitrogen), increasing their availability to Artemisia (Weaver 1930, Wraith et al. 1987, Miller et al. 1989). However, it was the shrubs on control plots which had higher (11%) nitrogen content than shrubs on defoliated plots in 1989 on the

native site. One explanation may be that denitrification reduced the amount of nitrogen available to shrubs on defoliated plots. Denitrification will increase when carbon in the soil increases (Westerman and Tucker 1978), which may have occurred due to death of grass roots caused by defoliation. The fact that nitrogen content in current year's growth was greater in shrubs on control than on defoliated plots on only one site, one year, may indicate that in the other instances nitrogen was not a limiting factor. Nitrogen content was not significantly different between treatments on the seeded site in 1989, or on either site in 1990. In the drought year, shrubs may not have been able to take advantage of an increase in soil nitrogen.

My prediction that defoliation of grass would increase soil resources available to associated shrubs was based on the principle of competitive production. I assumed that the two plant forms were competing with one another for resources, with negative impacts on each other's production, and that removal of the grass would therefore benefit the shrubs (or vice-versa). However, the principle of facilitative production, or facilitation (Vandermeer 1984b), may also have been important in the shrub-grass relationship. Facilitation is a change in environment caused by one species which benefits an associated species. Facilitation and competition can occur simultaneously, such that the net effect of the two processes can be either

positive, negative, or neutral. It is possible that the decline in nitrogen content for current year's growth in Artemisia on defoliated plots was caused by removal of a facilitation process provided by the grass. This process may have been more beneficial than competition was detrimental to shrubs on the control plots. The existence of facilitation relationships in rangeland plant communities is likely, and should be considered even when no net positive effect is realized.

I concluded that if there was an increase in soil moisture which I was unable to detect, the increase was too small to significantly affect the water potential, leaf conductance, growth, seedling survival or nitrogen content of associated shrubs. It is also possible that the amount of grass present in plots was too small to release substantial moisture to benefit associated undefoliated shrubs. Another possibility for the lack of shrub response to understory defoliation is that interspecific competition for soil resources may not have been a significant factor on Artemisia growth; intraspecific competition from neighboring Artemisia may have had an overriding influence. Fowler (1986) reviewed literature on plant competition and concluded that intraspecific competition was usually greater than interspecific competition.

Shrub Size Effects:

There was no difference in soil moisture content between small, medium and large shrub plots.

Large shrubs had equal or more negative (more stress) plant water potential than medium shrubs on all but one date, and equal or lower leaf conductance than medium shrubs on all but three dates. It could be that among larger, more mature Artemisia shrubs, intraspecific competition is greater than among smaller shrubs. This intraspecific competition may have been more intense and detrimental to health of large shrubs than interspecific competition was to that of smaller shrubs (Fowler 1986). If so, one could expect large shrubs to exhibit more water stress.

Another explanation for large shrubs exhibiting more water stress than medium shrubs is that large shrub canopies may be less water efficient than canopies of small shrubs. Small shrubs had visibly more dense canopies than large shrubs.

Drought Effects:

The second year of the study was a year of below average precipitation. I expected the drought to impair plant water relations, retard growth, and cause reduced nitrogen content in current year's growth. I thought there might be a change in the proportion of vegetative as opposed to reproductive growth, in the proportion of leaf versus

stem growth, and in the proportion of different leaf types. I also expected the effects of the drought might mask those of defoliation treatment and shrub size.

The first expectation of drought effects was realized. Artemisia water potential, leaf conductance, growth, and nitrogen content were reduced in the drought year. A water-stressed plant limits water loss by stomatal closure, resulting in reduced leaf conductance and carbon dioxide exchange, and ultimately reduced photosynthesis (Levitt 1980). Lack of sufficient water decreases cell turgor, with direct negative effects on plant water relations, and on cell expansion and plant growth. When moisture is limited, so is a plant's ability to use other soil resources, including nitrogen (Schulze 1991). Drought induces water stress in a plant, causing transfer of nitrogen from leaves and to roots and stems (Dina and Klickoff 1973).

The drought produced significant changes in the proportions of vegetative versus reproductive growth. The timing of development of various leaf and stem structures is a factor to consider when examining the response of plants to drought. Depending on the intensity and duration of the drought, as well as the influences of temperature and wind, development of certain structures may be retarded as the plant responds to stress with morphological plasticity. In the drought year, there was a proportionally greater reduction in weight and number of reproductive versus

vegetative leaves on the seeded site. We observed the same trend for stems as for leaves. It is common for plants subjected to environmental stresses such as drought to sacrifice reproductive development in favor of maintaining vegetative production (Chiariello and Gulmon 1991).

In the drought year compared to the previous growing season, plants allocated a larger proportion of resources for leaf growth than stem growth; that is, there was a reduction in stem development than in leaf development of reproductive shoots. This was also the case for vegetative shoots. Leaves may have been preferentially developed over stems to increase the energy return on carbon invested. The result of increased leaf:stem ratios in the drought year was that canopies were more densely arranged. This could lead to reduced wind and thus reduced evaporation within canopies during the drought year. Humidity would be higher in denser canopies, and water loss from stomata could decrease.

Proportion of annual versus ephemeral leaves on vegetative stems of shrubs on the seeded site changed in the drought year. There were proportionally more annual than ephemeral leaves in the dry year compared to the previous year. Ephemeral leaves are not as water-efficient as annual leaves (Miller and Shultz 1988), so the preferential allocation to annual leaves would seem a good strategy for water conservation.

CONCLUSION

The overall objective of this study was to quantify the response of Artemisia to defoliation of understory grasses. I monitored soil moisture and weather variables, and evaluated shrub parameters including water potential, leaf conductance, nitrogen content in current year's growth, annual biomass production, and seedling survival over a two year period. These parameters were also compared between shrubs of several size classes. As the second year of the study was considerably drier than the first, I was also able to quantify changes in Artemisia resulting from a drought.

Defoliation of understory vegetation as performed in this study had no significant effect on soil moisture, or on Artemisia water potential, leaf conductance, annual biomass production, or seedling survival. However, nitrogen content in current year's growth did respond to defoliation treatment; nitrogen content was elevated in the shrubs on control plots.

This research indicated that a single defoliation during the grass critical growing period was not sufficient to increase plant growth, reproductive effort or water status in Artemisia. One explanation for the lack of a positive shrub response to defoliation of herbaceous understory vegetation is that facilitation was as important as competition in the shrub-grass relationship. The

reduction in grass vigor may have resulted in a negative effect on Artemisia water status, growth and survival, such that no net positive effect from reduced competition was realized. The fact that shrubs on control plots had higher nitrogen content supports the facilitation theory.

I conclude that under the conditions of this study, defoliation did not increase the competitive advantage of Artemisia in the plant community. If herbivores are to be used as an economical method of controlling Artemisia through selective understory defoliation, future research must first address the extent to which a change in amount or timing of understory defoliation can produce a significant shrub response. Seedlings may be especially responsive to changes in timing of grass defoliation.

There were some differences in response of various shrub size classes. Larger shrubs tended to be more water stressed and produce less biomass than smaller shrubs, possibly due to less favorable root:shoot ratios, or less efficient canopy structure. The more negative (more stressed) water potentials and lower leaf conductance in large compared to medium shrubs are indicative of lower root:shoot ratios in the large shrubs. Canopies in the larger shrubs were less dense (fewer leaves per unit length of stem), which may have contributed to increased water loss, especially on hot or windy days.

The drought had predictable effects. Soil moisture content decreased, and Artemisia water potential, leaf conductance, nitrogen content in current year's growth, and annual biomass production were all lower in the drought year compared to the previous year. Plants living in semi-arid lands must adapt to survive highly variable environmental conditions. They often express morphological plasticity. This was evident in the current study. In the drought year compared to the previous year, there was an increase in proportional allocation to vegetative versus reproductive development, in number of annual versus ephemeral leaves, and in leaf versus stem development.

Drought is a common occurrence in the Great Basin. As such, it is important for land managers to understand the specific response of Artemisia to low soil moisture conditions. Some research has been done to determine if and how climatic conditions affect Artemisia succession. The reduction in allocation to reproduction seen in the current study indicates that dry years are probably not important for Artemisia seed production. However, future research on seed viability is necessary to determine the actual contribution Artemisia makes to the seed bank under varying climatic conditions.

The findings in this study elucidate several specific adaptations Artemisia possesses which enable it to survive in a semi-arid environment. The ability to alter amount of

carbon allocated to various plant parts in response to drought increases Artemisia's ability to compete successfully with other species for limited soil moisture.

Knowledge Artemisia response to defoliation of understory grasses and drought is useful when predicting trends in plant community succession and when planning management actions.

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APPENDIX

Appendix Table 1. Percent soil moisture content in the upper soil profile (20-200 mm) through the 1989 growing season on the seeded and native sites. Field capacity (-0.03 MPa) = 21% soil water content, wilting point (-1.5 MPa) = 9% soil water content.

Date	Seeded Site	Native Site
June 11	1.50 a	10.91 a
June 12	8.94 b	7.59 b
June 28	7.45 c	5.71 c
July 13	6.21 d	5.01 d
July 28	4.21 e	3.03 e
August 31	6.30	5.92
F-Value	348.50 *	226.07 *

*: Significantly different between dates on that site at $P \leq .10$; Numbers followed by same letter not significantly different between dates on that site; Numbers not followed by letters are means of 5 samples only; Values are means of 30 samples each date on seeded site, 20 samples per date on native site.

Appendix Table 2. Percent soil moisture content in the upper soil profile (20-200 mm) through the 1990 growing season on the seeded and native sites. Field capacity (-0.03 MPa) = 21% soil water content, wilting point (-1.5 MPa) = 9% soil water content.

Date	Seeded Site	Native Site
May 31	8.62 a	8.66 a
June 14	6.10 b	5.39 b
June 28	5.29 c	4.61 c
July 11	4.97 c	4.64 c
July 25	4.11 d	3.97 d
August 28	5.00 c	4.81 c
F-Value	190.02 *	138.44 *

*: Significantly different between dates on that site at $P \leq .10$; Numbers followed by same letter not significantly different between dates on that site; Values are means of 30 samples per date on seeded site, 20 samples per date on native site.

Appendix Table 3. Percent soil moisture content in the lower soil profile (200-400 mm) through the 1989 growing season on the seeded and native sites. Field capacity (-0.03 MPa) = 23% soil water content, wilting point (-1.5 MPa) = 10% soil water content.

SEEDED SITE:

Date	Mean	Std. Dev.	No. of Samples
June 11	3.96	1.66	30
June 12	12.16	1.98	30
June 28	9.91	1.55	29
July 13	8.27	1.34	25
July 28	7.95	0.98	13
August 31	7.76	0.46	4

NATIVE SITE:

Date	Mean	Std. Dev.	No. of Samples
May 31	15.88	2.01	20
June 14	11.21	1.65	20
June 28	8.67	1.79	19
July 11	8.68	1.76	15
July 25	6.96	0.95	3
August 28	6.91	1.65	5

Appendix Table 4. Percent soil moisture content in the lower soil profile (200-400 mm) through the 1990 growing season on the seeded and native sites. Field capacity (-0.03 MPa) = 23% soil water content, wilting point (-1.5 MPa) = 10% soil water content.

SEEDED SITE:

Date	Mean	Std. Dev.	No. of Samples
May 31	8.89	0.67	5
June 14	9.18	2.90	11

NATIVE SITE:

Date	Mean	Std. Dev.	No. of Samples
May 31	9.59	0.95	6
June 14	10.70	0.00	1

Appendix Table 5. Plant water potential (MPa) at pre-dawn (0400-0500 h) and mid-day (1200-1500 h) through the 1989 growing season for shrubs on the seeded and native sites.

PRE-DAWN:

Date	Seeded Site	Native Site
June 1	- .68 a	- .71 a
June 12	- .84 ab	- .94 b
June 28	- .91 b	-1.04 b
July 14	-1.19 c	-1.34 c
July 28	-1.58 d	-1.83 e
August 31	-1.27 c	-1.66 d
F-Value	34.14 #	82.65

MID-DAY:

Date	Seeded Site	Native Site
June 1	-1.49 a	-1.69 a
June 12	-1.80 b	-2.10 b
June 28	-1.75 b	-1.89 ab
July 14	-2.13 c	-2.64 c
July 28	-2.61 e	-3.15 d
August 31	-2.36 d	-2.78 c
F-Value	75.00	49.05

Numbers followed by contrasting letters significantly different at $P \leq .10$ between dates on that site; #: Significant interaction between date and size on this site; Values are means of 20 samples per site each date.

Appendix Table 6. Plant water potential (MPa) at pre-dawn (0400-0500 h) and mid-day (1200-1500 h) through the 1990 growing season for shrubs on the seeded and native sites.

PRE-DAWN:

Date	Seeded Site	Native Site
May 31	-1.30 a	-1.46 a
June 14	-2.04 c	-2.06 c
June 28	-2.48 d	-2.65 d
July 12	-2.93 e	-3.03 e
July 26	-3.49 f	-3.85 f
August 29	-1.68 b	-1.79 b
F-Value	195.22	133.35

MID-DAY:

Date	Seeded Site	Native Site
May 31	-1.75 a	-2.00 a
June 14	-3.00 c	-3.18 b
June 28	-3.40 d	-3.71 c
July 12	-4.22 e	-4.16 d
July 26	-4.34 e	-4.88 e
August 29	-2.73 b	-3.09 b
F-Value	278.37	92.95

Numbers followed by contrasting letters significantly different at $P \leq .10$ between dates on that site; Numbers followed by same letter not significantly different between dates on that site; Values are means of 20 samples per site each date.

Appendix Table 7. Leaf conductance (g cm^{-1} sec^{-1}) at morning (0730-0900 h) and afternoon (1200-1500 h) through the 1989 growing season for shrubs on the seeded and native sites.

MORNING:

Date	Seeded Site	Native Site
June 1	.52 a	.58 a
June 12	.54 a	.54 ab
June 28	.44 b	.48 b
July 14	.39 b	.38 c
July 28	.31 c	.35 c
August 31	.43 b	.28 d
F-Value	15.24	30.03

AFTERNOON:

Date	Seeded Site	Native Site
June 1	.48 a	.42 a
June 12	.42 a	.44 a
June 28	.29 bc	.43 a
July 14	.25 c	.24 b
July 28	.15 d	.24 b
August 31	.33 b	.27 b
F-Value	23.66	8.89

Values followed by contrasting letters significantly different at $P \leq .01$ between dates on that site; Values followed by same letter not significantly different between dates on that site; Values are means of 20 samples per site each date.

Appendix Table 8. Leaf conductance (g cm^{-1} sec^{-1}) at morning (0730-0900 h) and afternoon (1200-1500 h) through the 1990 growing season for shrubs on the seeded and native sites.

MORNING:

Date	Seeded Site	Native Site
June 14	.19 b	.25 b
June 28	.13 c	.10 c
July 12	.12 c	.11 c
July 26	.15 c	.13 c
August 29	.23 a	.32 a
F-Value	18.40	#74.94

AFTERNOON:

Date	Seeded Site	Native Site
June 14	.11 b	.11 b
June 28	.04 c	.00 c
July 12	.06 c	.06 bc
July 26	.10 b	.07 bc
August 29	.19 a	.27 a
F-Value	53.65	#48.75

Numbers followed by contrasting letters significantly different at $P \leq .10$ between dates on that site; Numbers followed by same letter not significantly different between dates on that site; #: Significant interaction between date and size on this site; Values are means of 20 samples per site each date.